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HOW THE NAIAD WAS DRAWN: A PRE-LINNEAN ICONOGRAPHY OF FRESHWATER MUSSELS

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ABSTRACT

This paper compiles the pre-Linnean iconography of freshwater mussels or naiads and provides an understanding of the historical framework in which they were created. The first book providing a figure of a freshwater mussel would seem to be *Hortus sanitatis*, an anonymous encyclopaedia first published in 1491. This and other early images of these animals related to the activity of obtaining pearls from *Margaritifera margaritifera*. The first traditional image of a freshwater mussel, drawn by Rondelet in 1555, was thereafter used by such other early naturalists as Boussuet, Gessner, Aldrovandi, and Jonston. The first microscopists Heide and Leeuwenhoek and pioneer malacologists Lister, D'Argenville and Ginanni were the first to depict the anatomy of naiads. We also have discovered a pre-Linnean image of a living naiad by Poupart showing its typical furrow in the sediments, and a pencil sketch by Linnaeus showing a pearl fishery of *M. margaritifera*.

Key words: pre-Linnean, history of malacology, Margaritiferidae, Unionidae, naiads.

INTRODUCTION

Long before a freshwater mussel or naiad was ever illustrated, the fossil record reflects a relationship between man and these bivalves. A recent analysis of aquatic fossils associated with hominids in the early Pleistocene of Trinil and Sangiran, Java, where the first fossil bones of *Homo erectus* were found, suggests that specimens of several freshwater mussel species from the nearby Solo River could have been deliberately caught by this hominid for consumption (Joordens et al., 2009), supported by the presence of many paired valves indicating that the molluscs were not dead and were transported by water before fossilization and by the complete absence of juvenile specimens, suggesting size-selective collection.

Later middens or accumulations of freshwater mussel shells have been discovered in ancient settlements of five continents, again suggesting that the soft parts of these animals were eaten. The shells could also be used as vessels, spoons, or other tools. Those middens include archaeological sites of the Palaeolithic, Neolithic, and Bronze ages in many parts of Europe (Locard, 1885; Hertel, 1956; Harrison et al., 1994; Cochet, 2005; Borrello & Girod, 2008) and Turkey, Syria and Jerusalem (Reese, 1990, 1995; Cartwright, 2003). They appear as well in Roman settlements (Sandberger, 1873; Kuipjer, 1988), Moorish settlements in Spain (Lozano et al., 2004), Egyptian tombs (Burleigh, 1983), Indian settlements in North America close to the Mississippi River and its tributaries (Matteson, 1953a, b; Hughes & Parmalee, 1999; Warren, 2000; Davis & Muehlenbachs, 2001), and Australian aboriginal settlements (Richards et al., 2007). Even today, freshwater mussels are a traditional source of food for Australian aborigines.

The first known shell collection, found at Pompeii and now housed in the Archaeological Museum of Naples, Italy, includes the freshwater mussel *Anodonta cygnea* (Linnaeus, 1758) (Damon, 1867; Tiberi, 1879; Dance, 1986).

Besides their use as food, the capacity of freshwater mussels to produce pearls has also generated great interest. Pearls were generically known in the Roman Empire as *margaritae*, but the word used for those of an exceptional size or quality was *unio*, which were unique and very valuable objects. The Romans imported marine pearls from the Red Sea and the Persian Gulf, but at least four Roman authors briefly mention the freshwater pearls of Britain: Gayus Suetonius (transl., 2004), Cornelius Tacitus (transl., 2010), Clau-

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dius Elianus (transl., 1984), and Gayus Plinius Secundus, better known as Pliny the Elder (transl., 1624; ed. 1992). Suetonius pointed out that, given his enthusiasm for pearls, Julius Caesar's main reason for invading Britannia in 55 B.C. was to gain control of its pearl rivers. According to Pliny, Caesar went to the temple of *Venus Genetrix* and dedicated to this Roman goddess a rich breastplate decorated with British pearls.

It was not, however, until the 13th century that the use of the word *pearl* and its French and Spanish variants *perle* and *perla*, all derived from the Latin *pirula* meaning "small pear", became the general term throughout Europe, replacing the word *margarita*. During the late Middle Age, European jewellers distinguished between so-called Oriental pearls, produced by the marine species *Pinctada margaritifera* (Linnaeus, 1758) and *P. radiata* (Leach, 1814), from the freshwater pearls produced by the European freshwater mussel *Margaritifera margaritifera* (Linnaeus, 1758). According to a document dated 1355, it seems that freshwater pearls were then preferred over marine pearls from India, the Red Sea, and the Persian Gulf, since the jewellers of Paris resolved not to mix the two types of pearl in items made of gold and silver, although an exception was made for large works for religious use (Landman et al., 2001).

The fishing and trading of the freshwater pearls of *M. margaritifera* since at least the 16th century are documented in Scandinavian rivers (Magnus, 1555), Scottish rivers (Geiger, 1637), and the Elster River and its tributaries in the Saxony Highlands (Rudau, 1961). All the pearls then fished in these and other European countries with *M. margaritifera* fisheries, such as Bavaria, Silesia, Bohemia, and Russia, were the property of emperors and kings, and there were heavy punishments for anyone found poaching.

In China, the earliest reference to freshwater pearls dates back to more than 4,000 years, according to the book on historical facts *Shu King*, in which King Yu is described to have received pearls from the Hwai River as a tribute (Donkin, 1998). The Chinese obtained marine pearls from southern China or imported them from Southeast Asia and the Persian Gulf, but even in remote antiquity, probably as early as the second or third century B.C., they had access to pearls from the freshwater mussels *Cristaria plicata* (Leach, 1814) and *Hyriopsis cumingii* (Lea, 1852), which are native to the Yangtse Delta and the rivers of central China. The species *M. margaritifera* was also exploited in the rivers of Manchuria and Korea, where there are records of the pearl extraction since the 14th century (Ziuganov et al., 1994).

There do not seem to be any representations of freshwater mussels by the old masters despite the use of the shells of these mussels, with their impermeable nacre lining, as vessels for mixing pigments and keeping the expensive golden powder. This use led to the designation *Conchae pictorum* [shells of painters] for naiads by almost all pre-Linnean naturalists. Later, Linnaeus chose the word *pictorum* to denote the *Unio pictorum* and assigned the name *anatina* [of ducks] to another naiad species in the genus *Anodonta*, alluding to its common use in some regions of Europe to feed ducks and pigs. In addition, he gave the name *cygnea* [of swans] to a similar, more slender and larger species of *Anodonta*.

Although a relationship between freshwater mussels and man is evident throughout prehistory and history, the first illustration of a specimen of this group of molluscs did not appear until the end of the 15th century. In the present paper, we show this and other figures to contribute to our knowledge of these animals and of pre-Linnean natural history.

MATERIAL AND METHODS

A search was conducted for images of naiads in friezes, sculptures, mosaics, bas-reliefs, and mural pictures from prehistory and Assyrian, Egyptian, Persian, Indian, Chinese, Greek, Etruscan, and Roman cultures. We also examined Gothic, Renaissance, and Baroque paintings, paying special attention to those of painters who commonly represented animals, such as Albrecht Dürer, Joris Hoefnagel, Daniel Fröschl, Rolandt Savery, Jan van Kessel, and other Flemish artists. Many drawings and engravings from the 16th to the 18th centuries were also checked for images of naiads, including old iconographical collections, such as the Van Berkheij's at the Museo Nacional de Ciencias Naturales, Madrid, Spain.

In an exhaustive bibliographic search, we reviewed books and documents prior to the printing in 1758 of the 10th edition of *Systema naturae* by Linnaeus, officially considered the start of zoological nomenclature. Due to the vast amount of literature examined, most of the old books and papers examined are not cited.

TABLE 1. Information on the pre-Linnean iconography of freshwater mussels.

Figure	Author	Date	Species name in the original	Modern name of species
Fig. 1	Anonymous	1491	*Eceo la concha margaritifera*	*Margaritifera margaritifera*
Fig. 2	Anonymous	1491	Untitled	*Margaritifera margaritifera* (pearl fishing)
Fig. 3	Magnus	1555	*De Margaritis & earum generatione*	*Margaritifera margaritifera* (pearl fishing)
Fig. 4	Geiger	1637	*Scottorum in fluviis piscandi modus*	*Margaritifera margaritifera* (pearl fishing)
Fig. 5	Rondelet	1555	*Musculis aquae dulcis*	*Anodonta* sp. (*anatina*?)
Fig. 6	Boussuet	1558	*Musculis aquae dulcis*	*Anodonta* sp. (*anatina*?)
Fig. 7	Gessner	1558	*Musculis aquae dulcis Rondeletius*	*Anodonta* sp. (*anatina*?)
Fig. 8	Aldrovandi	1606	*Musculus alter*	*Anodonta* sp. (*anatina*?)
Fig. 9	Jonston	1650	*Musculus Muschel*	*Anodonta* sp. (*anatina*?)
Fig. 10	Gessner	1558	*Conchae longae species, etc.*	*Margaritifera margaritifera*
Fig. 11	Aldrovandi	1606	*Concha longa zoographi*	*Margaritifera margaritifera*
Fig. 12	Lister	1678	*Musculus latus & Musculus angustior*	*Anodonta anatina & Unio pictorum*
Fig. 13	Buonanni	1681	*Concha longa, pictorum dicta*	*Unio pictorum*
Fig. 14	Buonanni	1709	*Concha longa, pictorum dicta*	*Unio pictorum*
Fig. 15	Lister	1681	*Musculus, etc.*	*M. margaritifera, A. anatina. & U. pictorum*
Fig. 16	Lister	1685–1692	*Musculus niger, etc.*	*Margaritifera margaritifera*
Fig. 17	Lister	1685–1692	*Musculus angustior, etc.*	*Unio pictorum*
Fig. 18	Lister	1685–1692	*Musculus latus, maximus, etc.*	*Anodonta* sp. (*cygnea*?)
Fig. 19	Lister	1685–1692	*Musculus tenuis, minor, etc.*	*Anodonta anatina*
Fig. 20	Lister	1685–1692	*Musculus fluviatiles, é Fluvio Tamesi*	Deformed specimen
Figs. 21–26	Lister	1685–1692	*Musculus, etc. & Pectunculus, etc.*	Several unidentified species
Fig. 27	Lister	1685–1692	*Pectunculus subviridis, triquetrus*	See comment on this figure in text
Fig. 28	Lister	1685–1692	*Musculus, a Danubio*	*Unio tumidus*
Fig. 29	Lister	1696	*Musculi fluviatilis anatome*	Unionidae (anatomy, glochidia, shell crystals)

(continues)

(continued)

Figure	Author	Date	Species name in the original	Modern name of species
Not figured	De Heide	1683	*Mytuli, Belgicè mossel*	*Anodonta anatina* (isolated parts)
Fig. 30	Van Leeuwenhoek	1697	*Veen-Oesters or Mosselen*	*Anodonta cygnea* (anatomy and embryos)
Fig. 31A	Poupart	1731	*Moule*	*Anodonta anatina*
Fig. 31B	Poupart	1731	*Moule*	Unidentified Unionidae (specimen track)
Not figured	Scheuchzer	1735	*Fluss-Muschel, Musculus Fluviatilen*	Unidentified Unionidae (specimen track)
Fig. 32	Anomymous	1736	*Hüte Dich fur Schaden*	*Margaritifera margaritifera* (pearl fishing)
Fig. 33	Anonymous	circa 1760	*Perlen-Sucher, etc.*	*Margaritifera margaritifera* (pearl fishing)
Fig. 34	Linnaeus	1732	Untitled	*Margaritifera margaritifera* (pearl fishing)
Fig. 35	Hermann	1737	*Concha fluviatiles margaritifera, etc.*	*Margaritifera margaritifera* (anatomy)
Fig. 36	Gualtieri	1742	*Musculus fluviatilis, etc.*	*Unio* sp. & *Anodonta cygnea*
Fig. 37	D’Argenville	1742	*Moules*	Several unidentified species
Fig. 38	D’Argenville	1757	*Moules*	Several unidentified species (living specimens)
Fig. 39	D’Argenville	1780	*Moules*	Several unidentified species
Fig. 40	Marsigli	1744	*Moule*	*Unio* sp.
Fig. 41	Swammerdam	1737	*Een Holandische Mossel*	Unidentified Unionidae (soft parts)
Fig. 42	Klein	1753	*Diconcha sulcata*	*Margaritifera margaritifera*
Fig. 43	Klein	1753	*Musculus latus*	*Anodonta anatina*
Fig. 44	Valentijn	1754	Untitled	*Unio pictorum*
Fig. 45	Pontoppidan	1755	*Freshwater muscle & pearls*	*Margaritifera margaritifera* (pearls)
Fig. 46	Ginanni	1757	*Conca de Pittori*	*Anodonta anatina* (soft parts)
Fig. 47	Ginanni	1757	*Conca de Pittori*	*Unio* sp. (*pictorum*?)
Fig. 48	Adanson	1757	*Le Mutel*	Unidentified Mutelidae
Fig. 49	Knorr	1768	*La Moule a perles de l’Elster*	*Margaritifera margaritifera*

The following are the types of bibliographic sources included: (1) old editions by authors who wrote about natural history, such as Aristotle (transl., 1970), Pliny, Elianus, Dioscoride, Albertus Magnus, Vincent de Beauvois, Konrad von Megenberg, Clusius; (2) Medieval and Renaissance bestiaries and *Physiologus* of Oxford, Cambridge, Westminster, Bern, El Escorial, Juan de Austria, Rudolph II of Habsburg; (3) *Cosmographies* by Münster and Thevet; (4) catalogues of the old *Kunstkammern* by Imperato, Ceruti, Tradescant, Worm, Moscardo, Terzago, Olearius, Legati, Grew, Dumolinet, Kircher, Buonanni, Valentini, Besler, Vincent, Seba, Gersaint; (5) books devoted to invertebrates or aquatic animals by Belon, Rondelet, Boussuet, Salviani, Mattioli, Gessner, Aldrovandi, Colonna, Jonston, Petiver, Redi; (6) books on gemology and margaritology by Boodt and Geiger, as well as modern books on pearls by Donkin (1998), Joyce & Addison (1993), Landman et al. (2001); (7) dissertations and opuscules on the nature of pearls and their formation by Hermann, Zschau, Oertel, Plot, Réaumur and other 18th century authors, including the information at the *Encyclopédie* by Diderot, D´Alembert, and Jaucourt; (8) other opuscules on mussels and bivalves by Heide, Poupart, Méry; (9) pre-Linnean books on malacology and conchology by Buonanni, Lister, Rumpf, Gualtieri, D'Argenville, Adanson, Knorr, Regenfuss; (10) modern books dealing with paintings of still lives and of shells.

Especially useful for our research were the bibliographic references given by Lister (1692–1697) in the second edition of *Historia conchyliorum*, by Regenfuss (1758), and by Schröter (1779). Also of great help have been the compilations of zoological iconography by Barbero (1999) and on the ancient malacological bibliography by Caprotti (1994), the catalogue of special funds of the Library of the Museo Nacional de Ciencias Naturales of Madrid (Vicente & Orbiso, 1990; Vicente et al., 1992, 1998; Orbiso et al., 2000), and electronic versions of the catalogues of the British Library, London, England, the Gallica National Library, Paris, France, the National Library of Madrid and the Library of the Consejo Superior de Investigaciones Científicas in Spain.

Some of the original figures reproduced here have been slightly modified for reasons of space.

PRELINNEAN ICONOGRAPHY OF FRESHWATER MUSSELS

The first book in which a figure of a freshwater mussel was provided (Table 1) seems to be *Hortus sanitatis*, an zoological and botanical encyclopaedia, first published in 1491 in Mainz, Germany, with later editions (Anonymous, 1491). This book has been claimed to have been written by a German physician named Johann Wonnecke von Caub or Johannes de Cuba. In a chapter entitled *Tractatus de piscibus*, there is a woodcut showing several fishes together with three elongate bivalves with extended mantles and feet (Fig. 1). The figure suggests today's well-known relationship between naiads and fishes. An accompanying text reads *Eceo la concha margaritifera* [here is the pearl-producing shell] alluding to *M. margaritifera*. Another picture (Fig. 2) in a chapter entitled *De lapidibus*, shows a man extracting a pearl from a mussel with another pearl in the other hand probably being subjected to the so called "tooth test".

In chronological order, the next book to consider is *Historia de gentibus septentrionalibus* by Olaus Magnus, a catholic bishop of Uppsala, Sweden, who later moved to Rome. The first edition appeared in 1555 and was followed by several others. One of its many small woodcuts showed a scene of a pearl fishery in a river under the title *De margaritis et earum generatione* [on pearls and their origin] (Fig. 3). It also showed sumptuary objects related to pearls, such as rings, strings, crowns, and jewel cases. The sun shining over the scene probably alludes to Pliny's theory on the origin of pearls, according to which mothers of pearls come to the water surface, take in the dewdrops, and generate pearls after being fertilized by a sun ray. A flying bird, probably a kingfisher, carries a naiad in its beak in another reference to this theory. Similar yet different scenes appear in other editions.

Another scene of a pearl fishery in a river can be found in *Margaritologia, sive dissertatio de margaritis*. This book, printed in 1637, was the first exclusively devoted to pearls and their medical uses. Its author was Malachias Geiger, physician to Emperor Rudolph II of Habsburg. Anselmus Boetius de Boodt (1609) was also physician to that emperor and also published a treatise on gems and pearls, but

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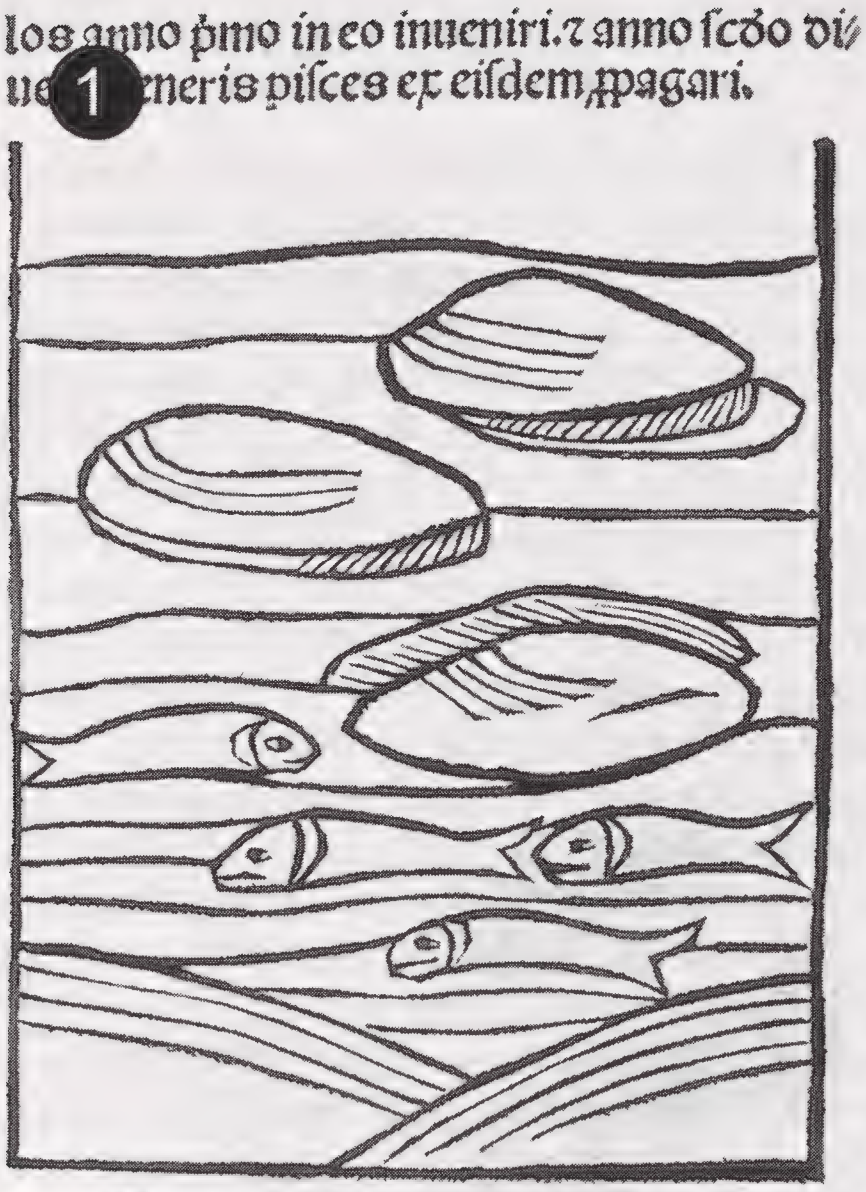

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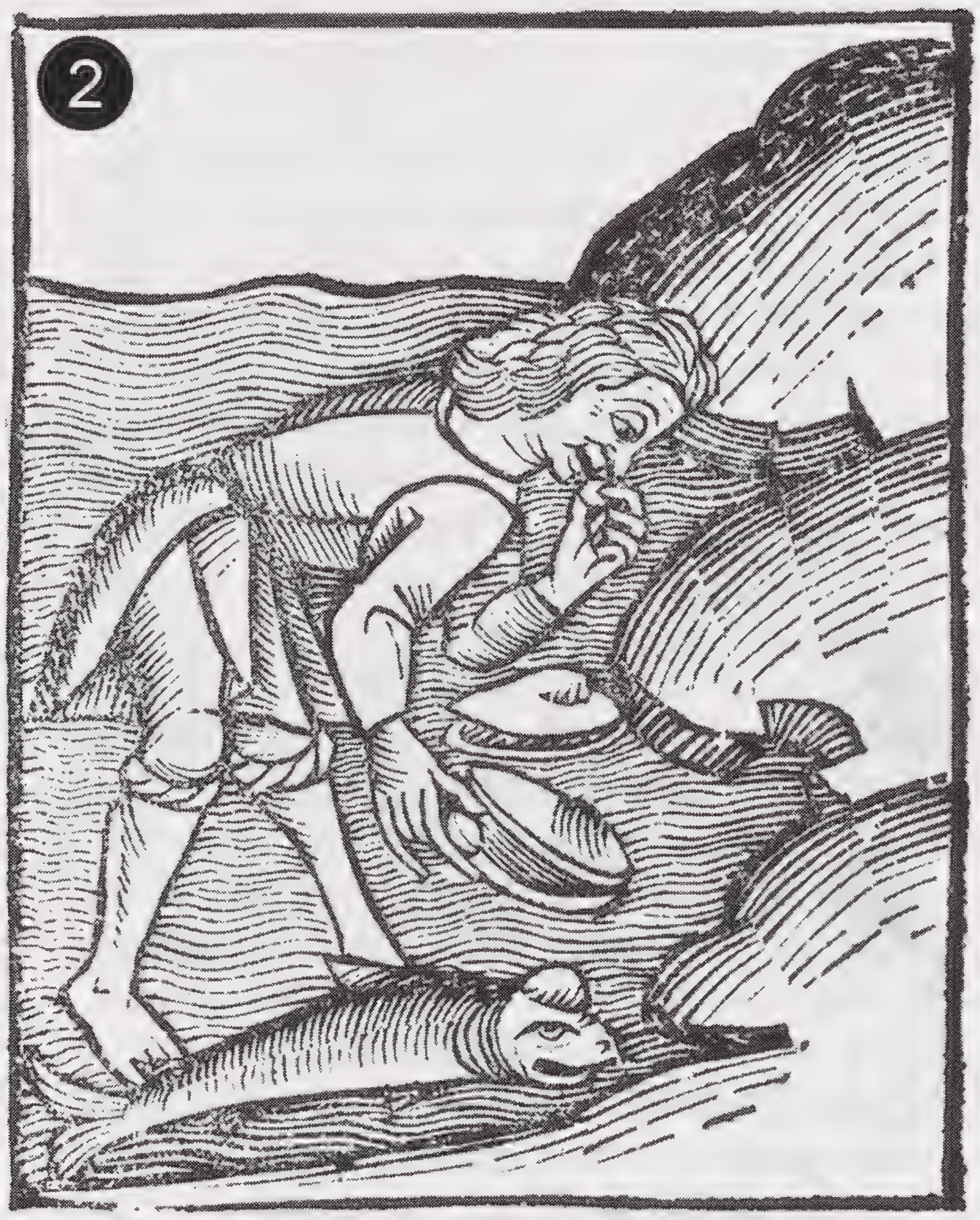

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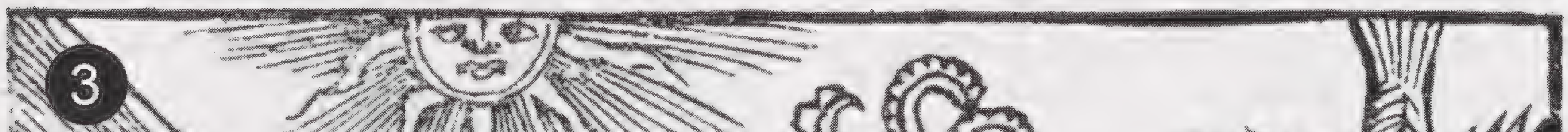
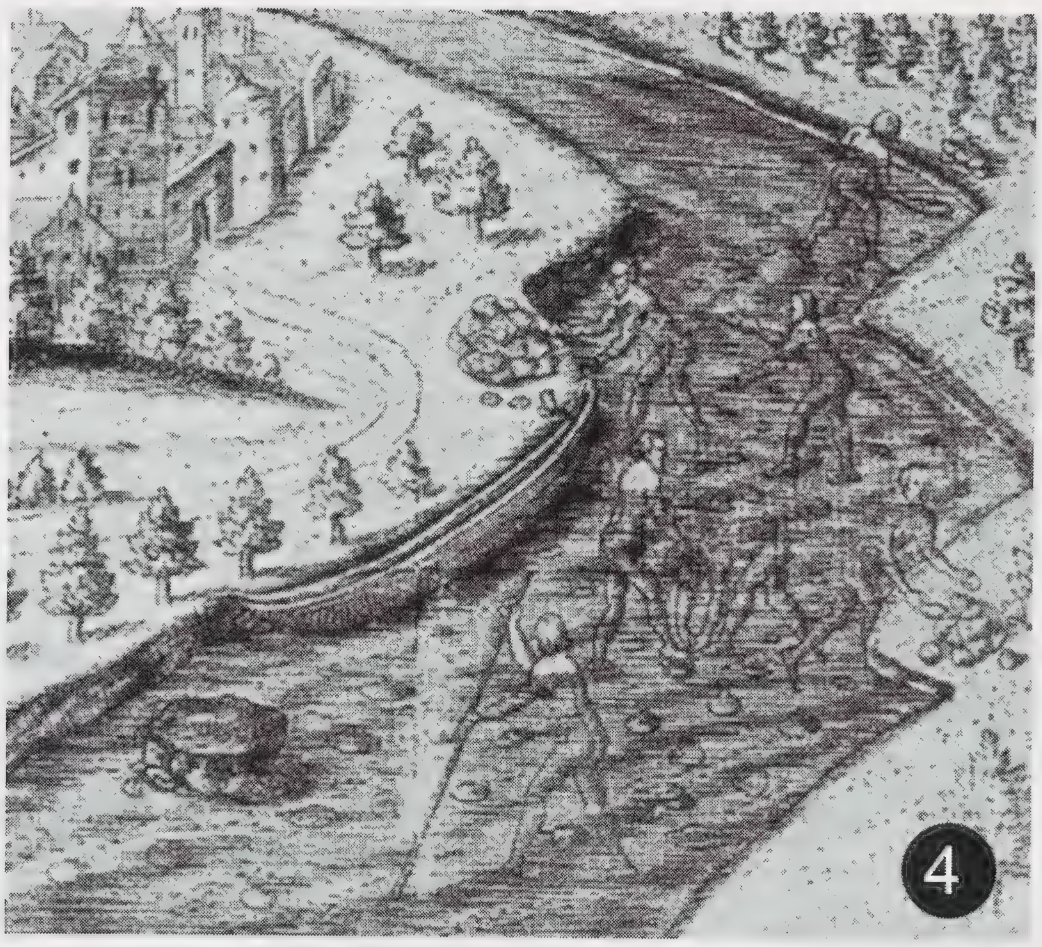
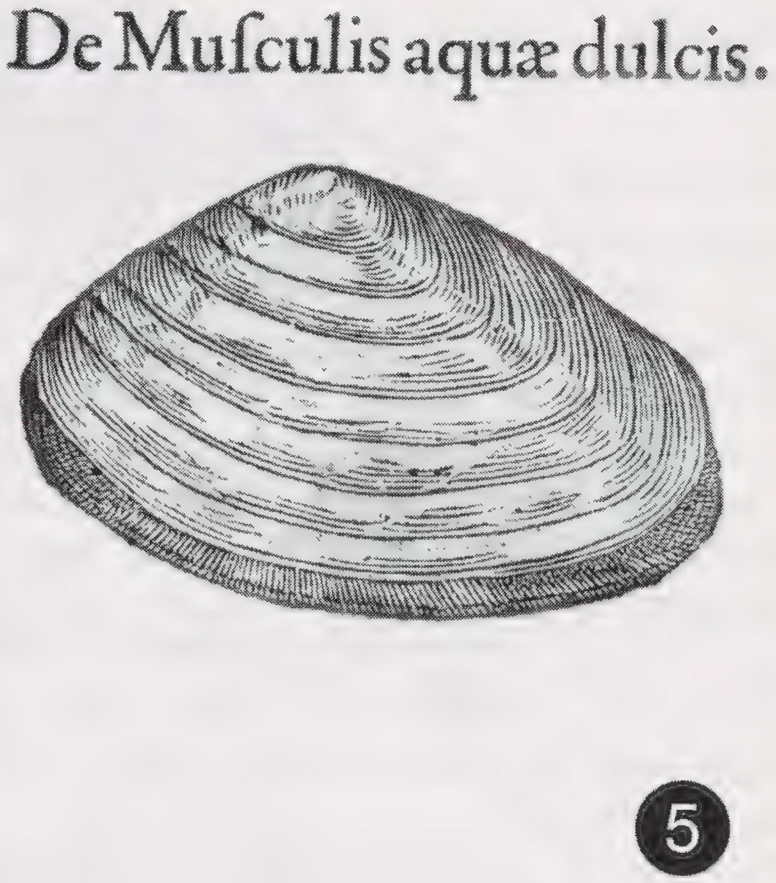
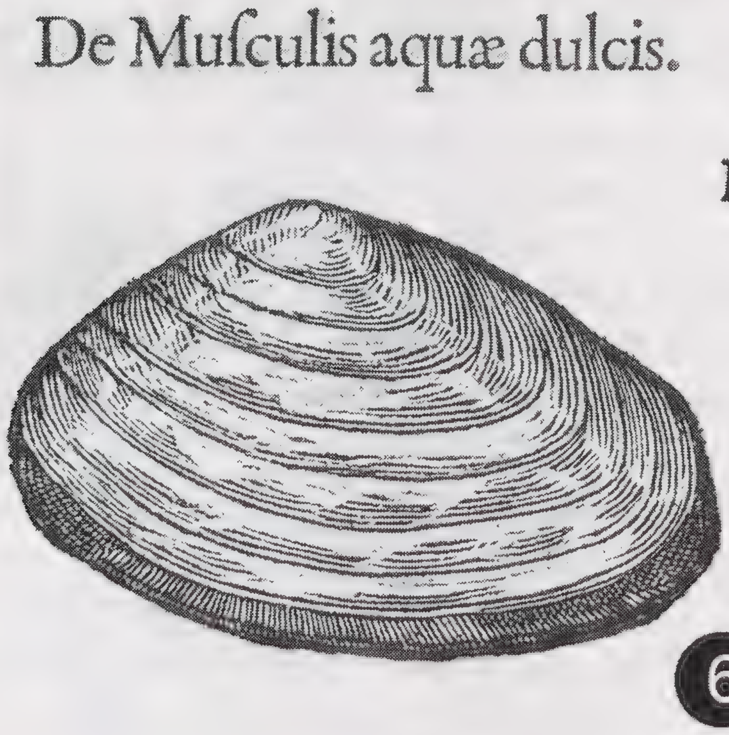


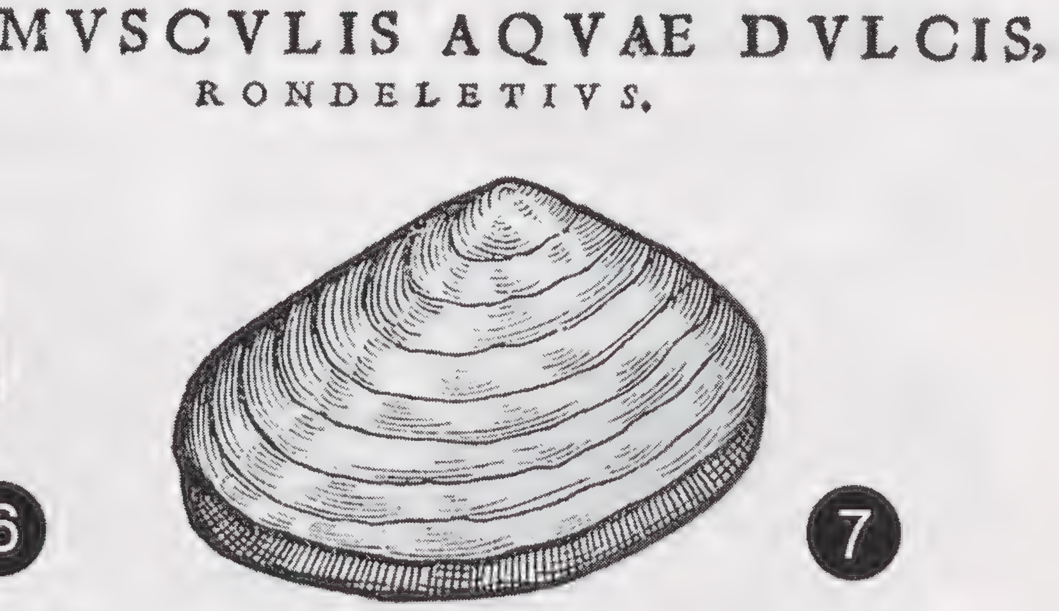
De Margaritis, & earum generatione.

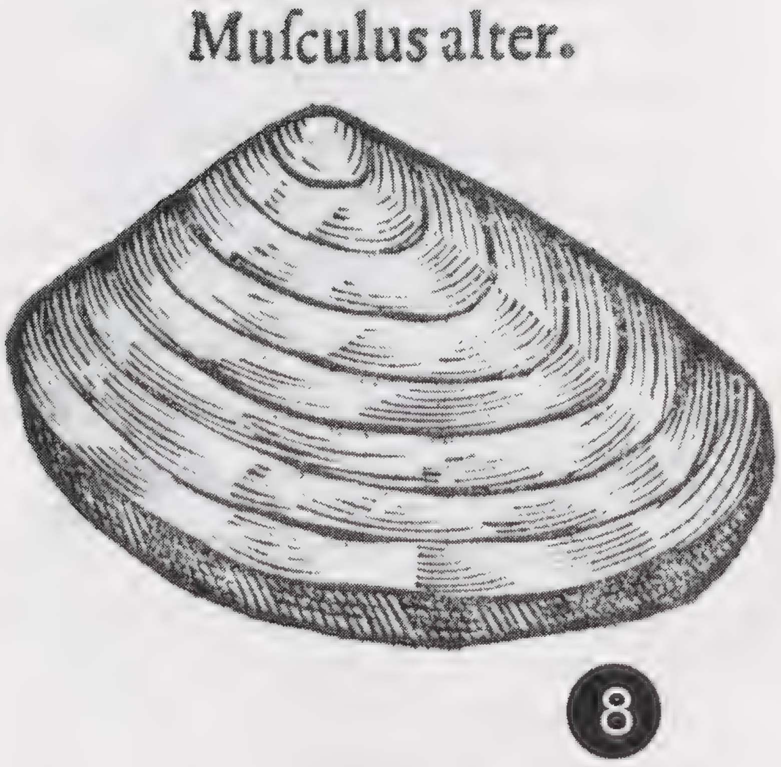
FIGS. 1–3. FIG. 1: *Concha margaritifera* from *Hortus sanitatis* (Anonymous, 1491); FIG. 2: Other image supposedly representing *Margaritifera margaritifera* from *Hortus sanitatis* (1491); FIG. 3: A fishery of *Margaritifera margaritifera* from Magnus (1555). FIGS. 1–3: By permission of Biblioteca Nacional, Madrid, Spain.

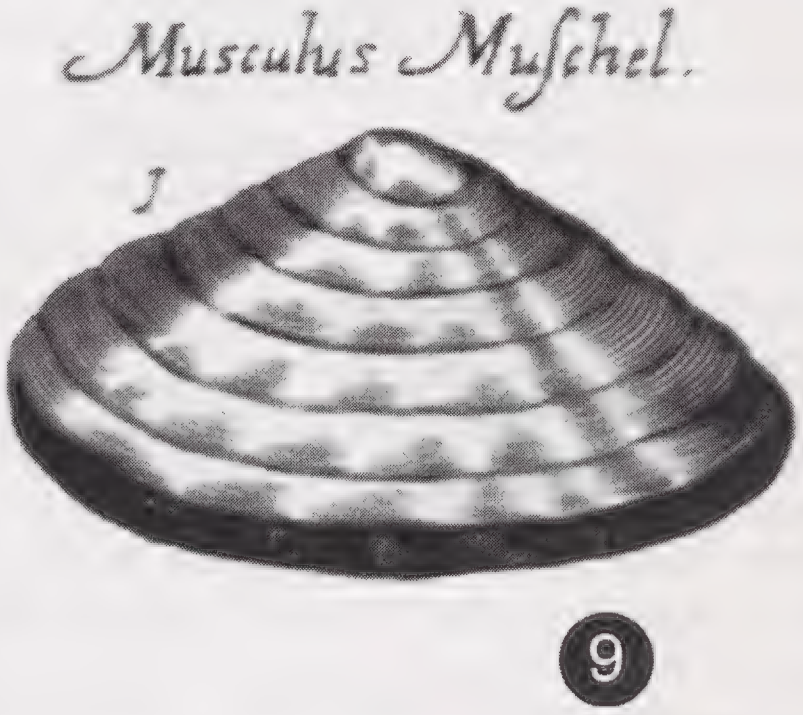












FIGS. 4–9. FIG. 4: A fishing pearls scene in a river of Scotland from Geiger (1637); FIG. 5: *Musculus aquae dulcis* from Rondelet (1555); FIG. 6: *Musculus aquae dulcis* from Boussuet (1558); FIG. 7: *Musculus aquae dulcis* from Gessner (1558); FIG. 8: *Musculus* from Aldrovandi (1606); FIG. 9: *Musculus* or *Muschel* from Jonston (1650). FIGS. 5–8: By permission of Museo Nacional de Ciencias Naturales, Madrid, Spain; FIG. 9: By permission of Biblioteca Nacional, Madrid, Spain.

it lacked images of naiads. A folded plate in Geiger (1637) represents four ways of obtaining pearls in different parts of the World. The fourth manner (Fig. 4) was referred to as *Scottorum in fluviis piscandi modus* [fishing in rivers in the Scottish way].

The first canonical image of a freshwater mussel can be found in *Universae aquatilum historia* by Rondelet (1555), the second part of *Libri de piscibus marinis* by this author, who was a professor of medicine at the University of Montpellier, France. The triangular shape of a shell there named *Musculis aquae dulcis* [freshwater mussel] (Fig. 5) suggests it is a specimen of *Anodonta anatina*. The Latin text explains that its flesh is hard, difficult to cook, foul tasting and that its juices could produce fever. These last words are the first medical reference to the capacity of freshwater mussels, as filter feeding organisms, to accumulate bacteria and viruses, causing such infectious diseases as gastroenteritis, typhoid fever, cholera, and hepatitis.

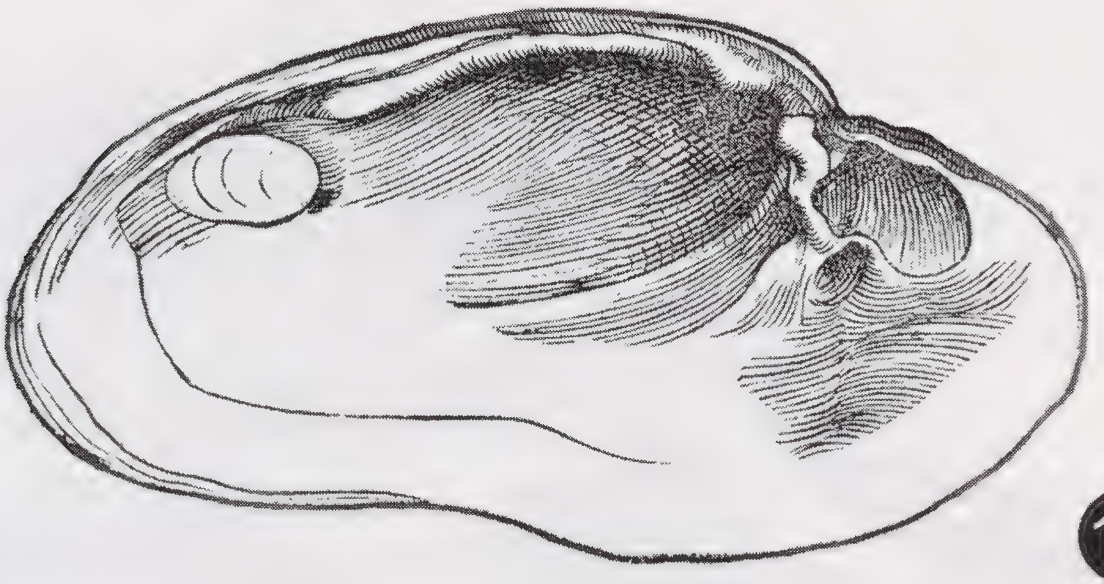
This image by Rondelet (1555) was repeated by Boussuet (1558) (Fig. 6), because Matthias Bonhomme, an editor from Lyons, France, who printed both books, used the same woodcuts to illustrate them. The picture was also copied and printed as a mirror image by the Swiss doctor and naturalist Konrad Gessner (1558) for *De aquatilibus* (Fig. 7), the fourth book of his famous *Historia animalium*, a work that saw later editions (Gessner, 1560, 1563), the first one only including the iconographical part and short commenting texts. Two more drawings of Rondelet's *Musculis aquae dulcis* were provided by Ulisse Aldrovandi (1606) (Fig. 8), professor of medicine at the University of Bologna, Italy, and by John Jonston (1650) (Fig. 9), a Polish physician and naturalist established in England. Interestingly, two other figures by Jonston named *Concha margaritifera* and *Concha pictorum* are not naiads, despite their names, but rather the marine bivalves *Pinctada margartitifera* and *Anomia ephippium* (Linnaeus, 1758).

An unmistakable, often copied image of a freshwater mussel was originally figured by Gessner (1558). This figure showed the inner side of a left valve of *M. margaritifera* (Fig. 10) with a caption reading *Conchae longae species etiam in dulcibus aquis reperitur* [long-shelled species also found in freshwater]. The attached text speaks of *Concha pictorum* [shell of painters]. As happened with the above-mentioned figure of *Musculis aquae dulcis Rondeletius* [freshwater mussel according to Rondelet], this figure by Gessner was copied by Aldrovandi (1606) (Fig. 11) and inspired later drawings by such authors as Lister, Klein, and Knorr, as discussed below.

The British physician and naturalist Martin Lister was a fellow and then vice-president of the Royal Society of London and author of a monumental malacological work. His *Historia animalium Angliae* (1678) illustrated in four figures the inner and outer sides of *Anodonta* sp. and *Unio pictorum* (Fig. 12), which Lister respectively named *Musculus latus* [broad mussel] and *Musculus angustior* [narrow mussel]. These pictures of *Unio* by Lister (1678) were used by Filippo Buonanni (1681) for his *Ricreatione dell´occhio e della mente nell´osservatione delle chiocciole* (Fig. 13), the first book entirely devoted to shells. Its Italian edition was followed by a Latin one in 1684. Buonanni was a Jesuit priest who succeeded the Jesuit and erudite Athanasius Kircher as director of the *Kunstkammer* at *Collegium Romanum*, better known as Kircher's Museum. A remake of the same *Unio* figures appeared in *Icones testaceorum* (Fig. 14), the last part of *Musaeum Kircherianum*, a catalogue by Buonanni (1709) of the items displayed in that museum.

Lister's *Appendix ad Historiam animalium Angliae* (1681) contained a folding plate in which the author represented several British naiads (Fig. 15). One of these was a drawing of the inner side of a left valve of *M. margaritifera*, named *Musculus niger, omnium longe crassisimus, conchae longae species Gesn. Aldrov.* [black mussel, thick over its entire length, long-shelled species according to Gessner and Aldrovandi]. There also appeared the figures of two *Anodonta*, respectively named *Musculus tenuis minor* [thin small mussel] and *Musculus tenuis maximus* [thin great mussel], and two *Unio pictorum*, named *Musculus ex viridi, pallidus, omnium angustissimus* [very narrow mussel, pale green] and *Musculus angustior, ex flavo seu viridi nigricans* [narrow mussel, as often yellow as blackish green].

The monumental *Historia conchyliorum* by Lister was the first serious attempt to classify and illustrate all the testacean molluscs then known. It contained a thousand engravings after drawings by Anna and Susanne Lister, wife and daughter of this author. The first edition was printed in London in 1685–1692 and was soon followed by a second one in 1692–1697. A third, luxury edition appeared in Oxford in 1770. This was devoted to the second



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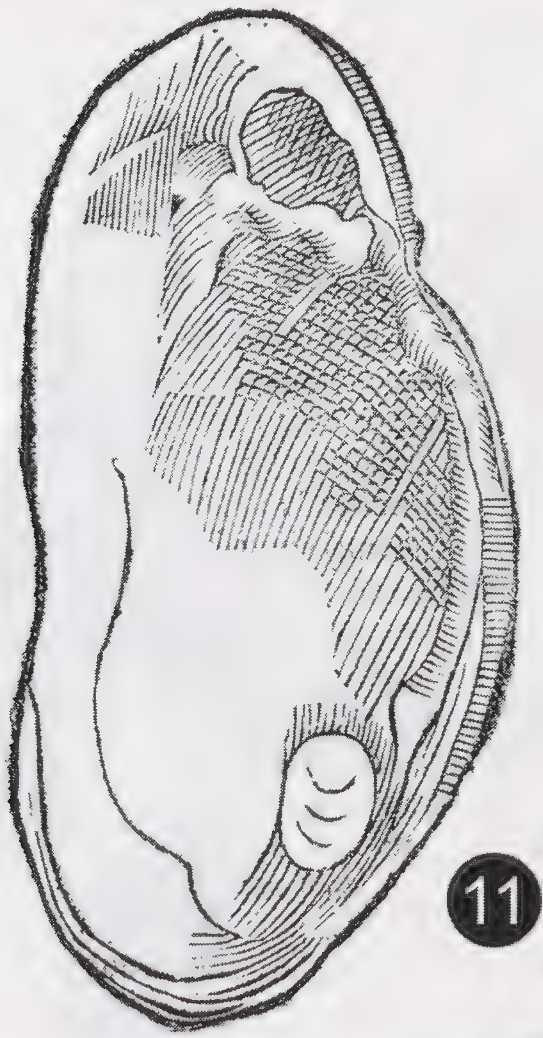
Conchæ longæ ſpecies etiam in dulcibus aquis reperitur: cuius teſtam alteram parte eius interna

Concha longa Zoographi.



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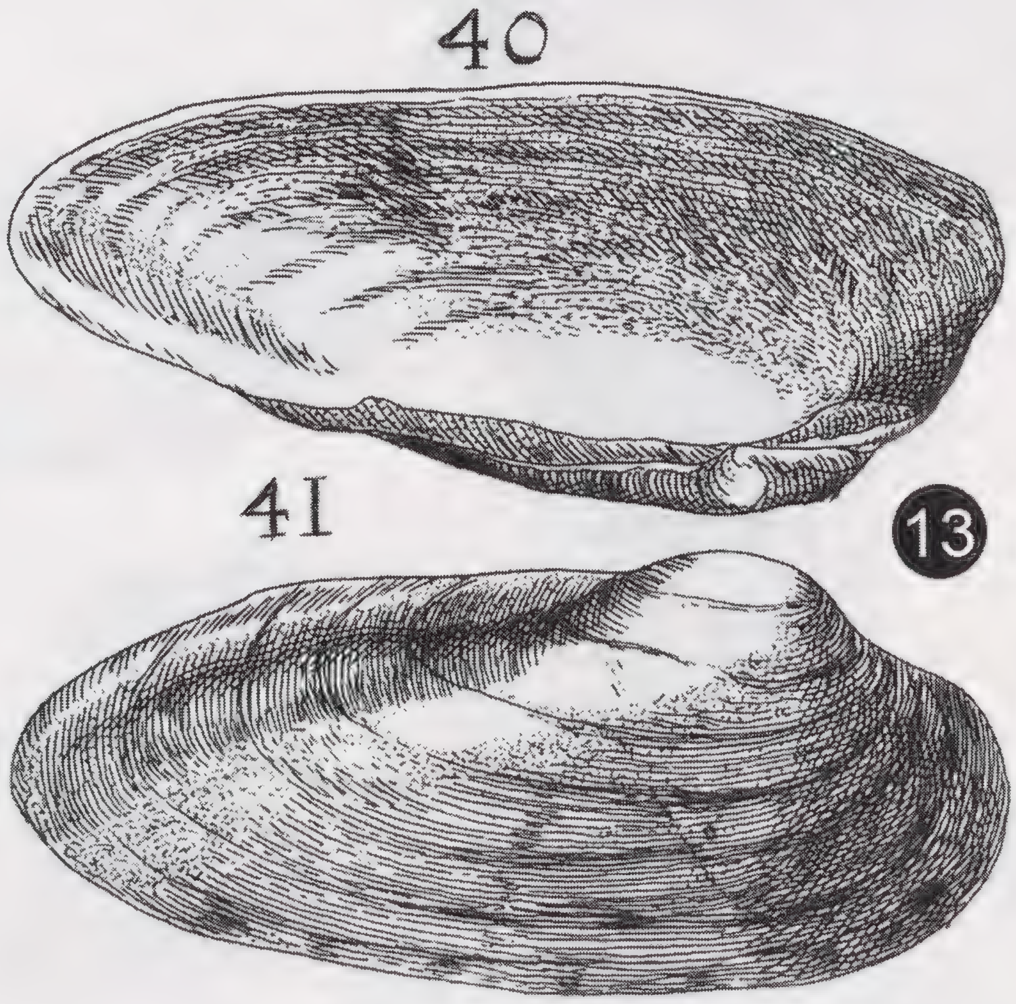

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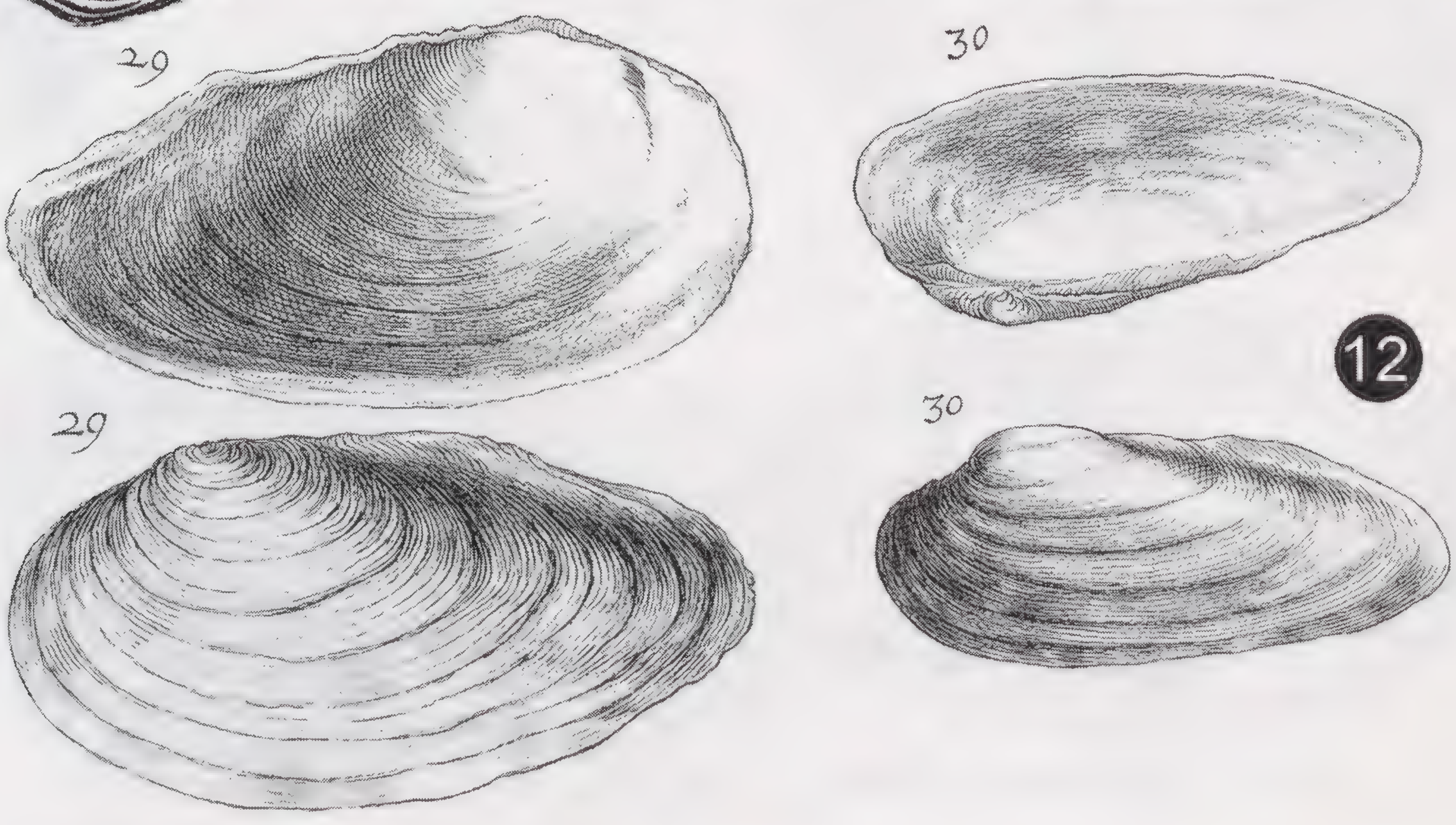
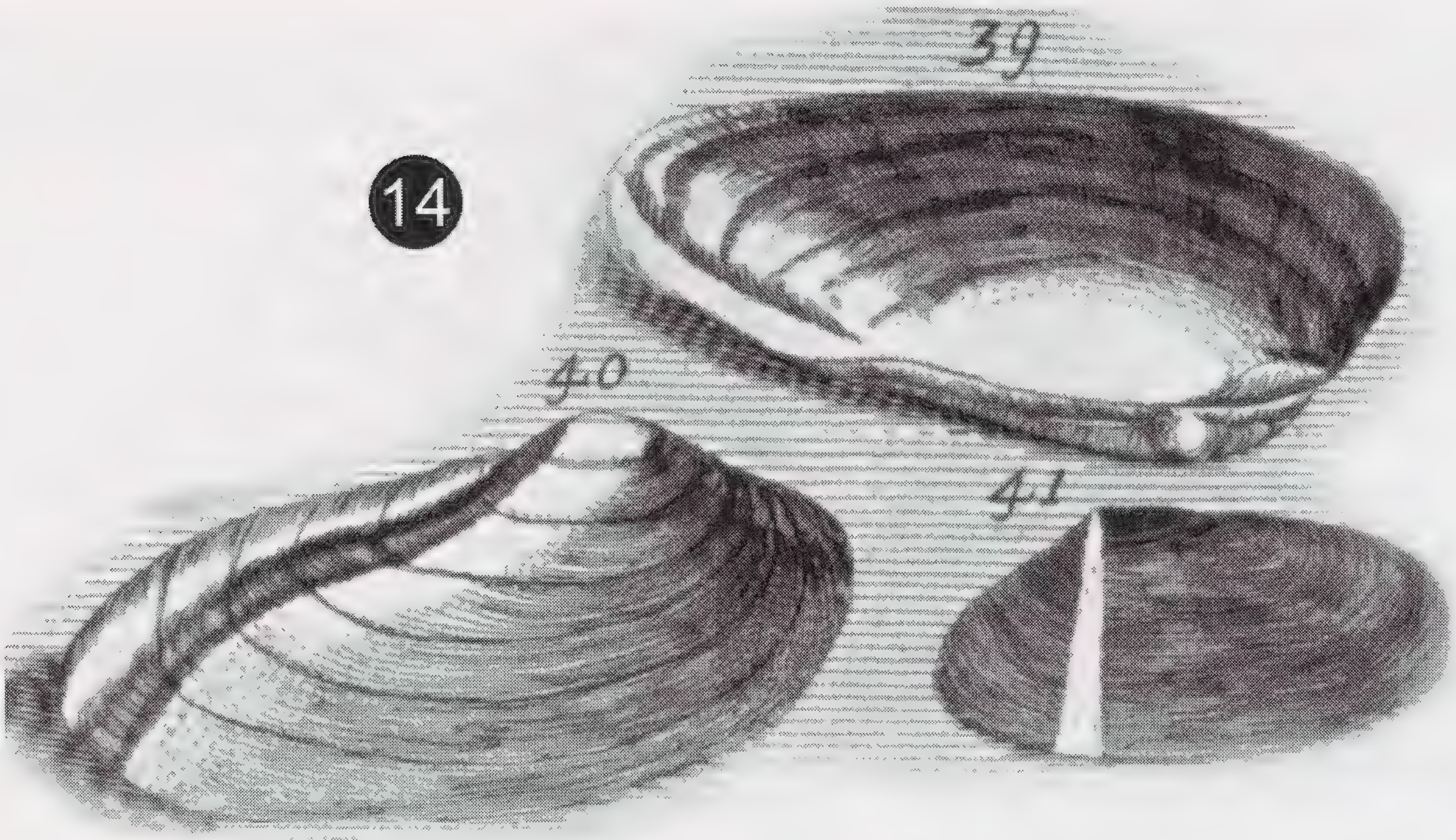
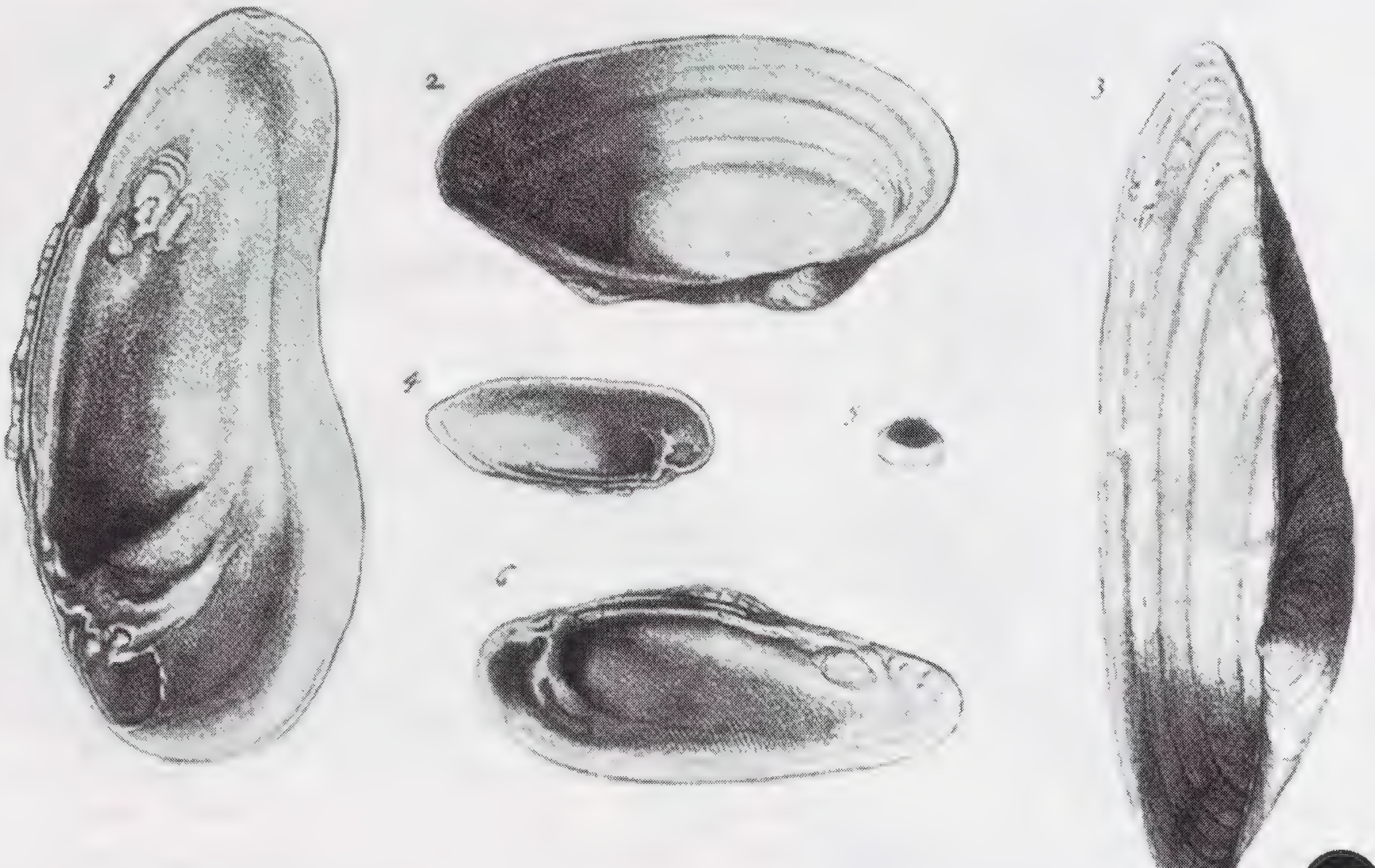


12

FIGS. 10–13. FIG. 10: *Conchae longae species etiam in dulcibus aquis reperitur* from Gessner (1558); FIG. 11: *Concha longa* from Aldrovandi (1606); FIG. 12: *Musculus latus* and *Musculus angustior* from Lister (1678); FIG. 13: *Concha longa, pictorum dicta* from Buonanni (1681). FIGS. 10–12: By permission of Museo Nacional de Ciencias Naturales, Madrid, Spain; FIG. 13: By permission of Biblioteca Nacional, Madrid, Spain.

14





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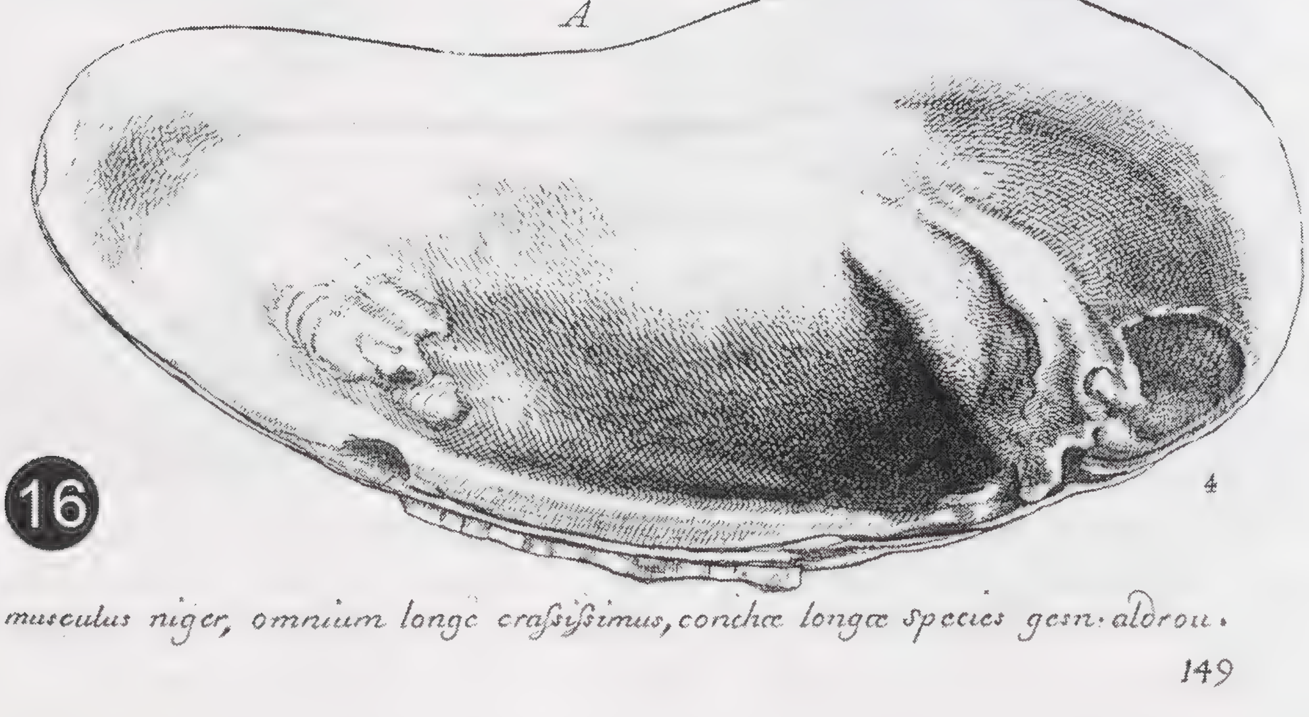
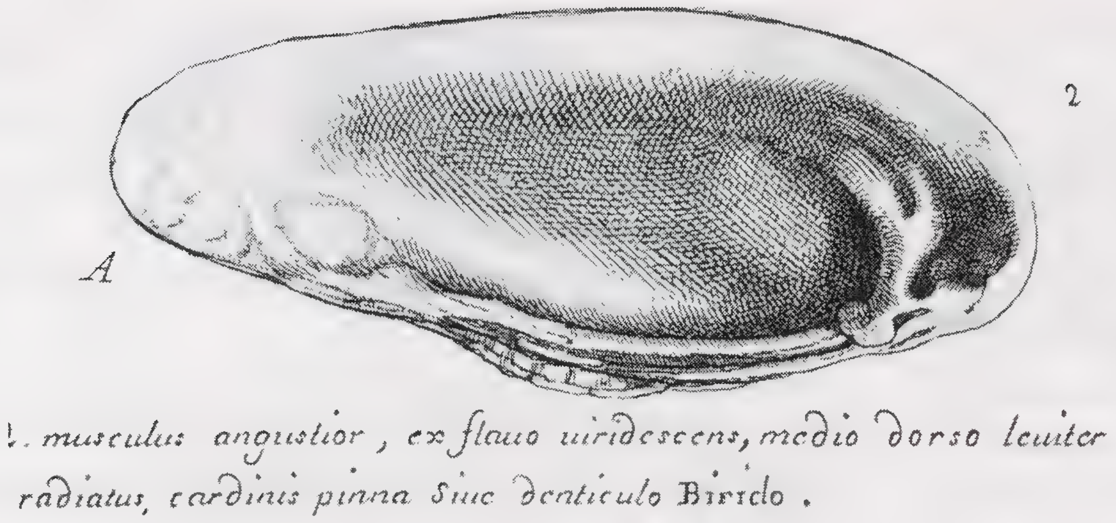
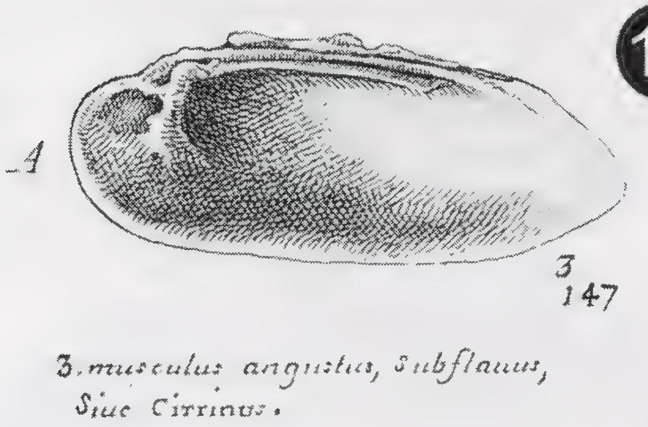
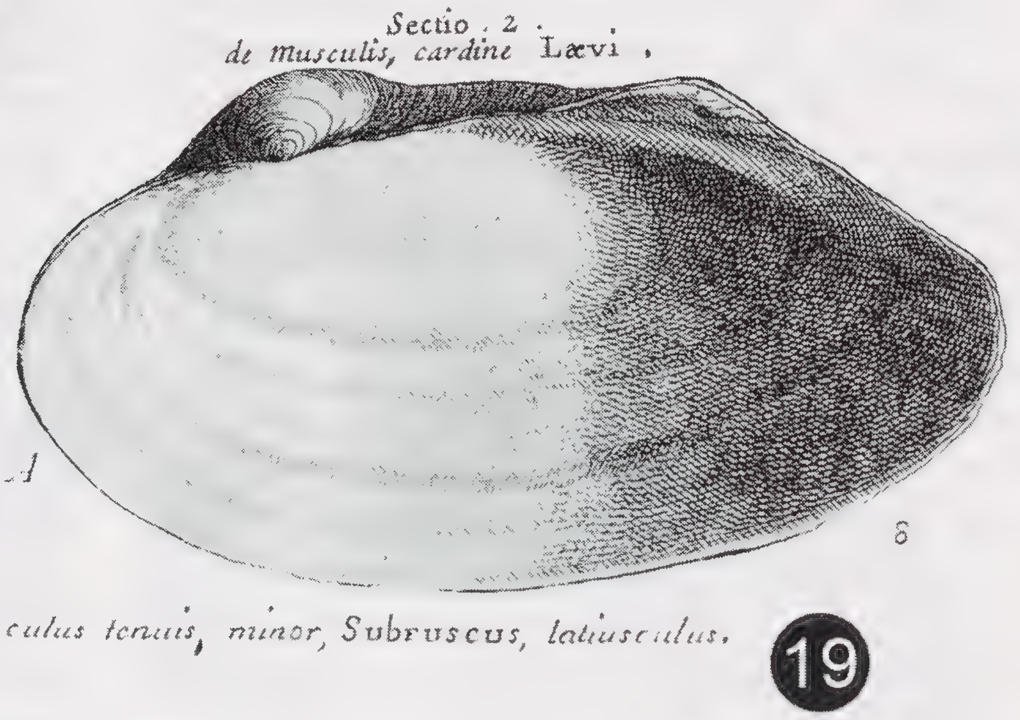

A
4
4. musculus niger, omnium longe craſsiſsimus, conchæ longæ species gesn. aldrou.
149

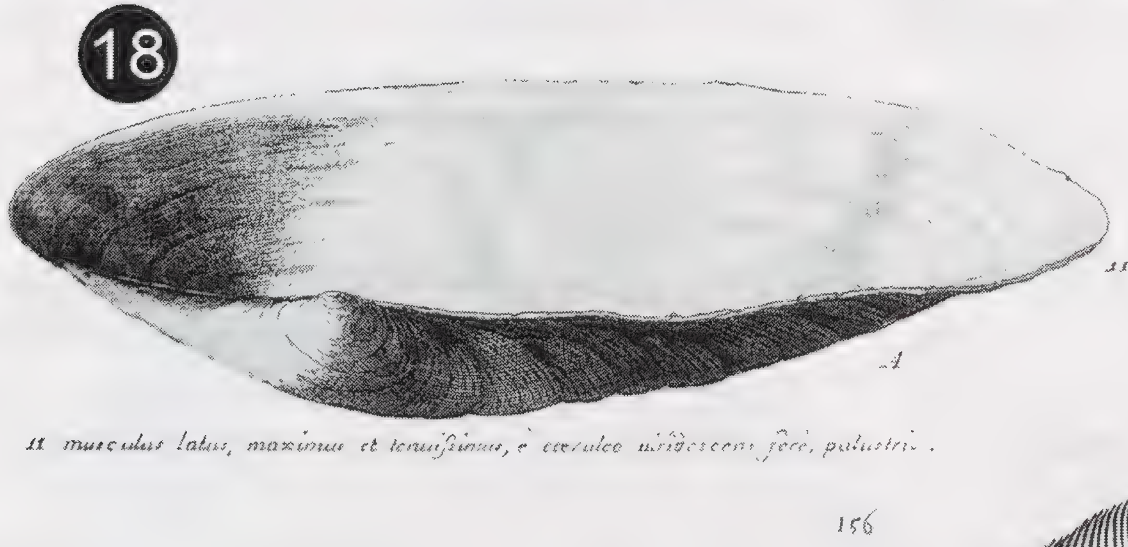
16

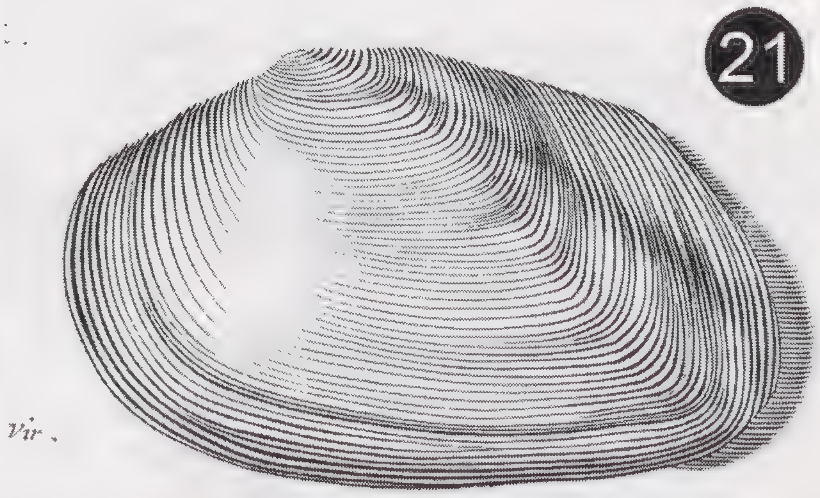
FIGS. 14–16. FIG. 14: *Concha longa, pictorum dicta* from Buonanni (1709); FIG. 15: Figures of several British freshwater mussels from Lister (1681); FIG. 16: Figure of *Margaritifera margaritifera* from Lister (1685–1692). FIGS. 14, 15: By permission of Biblioteca Nacional, Madrid, Spain; FIG. 16: By permission of Museo Nacional de Ciencias Naturales, Madrid, Spain.

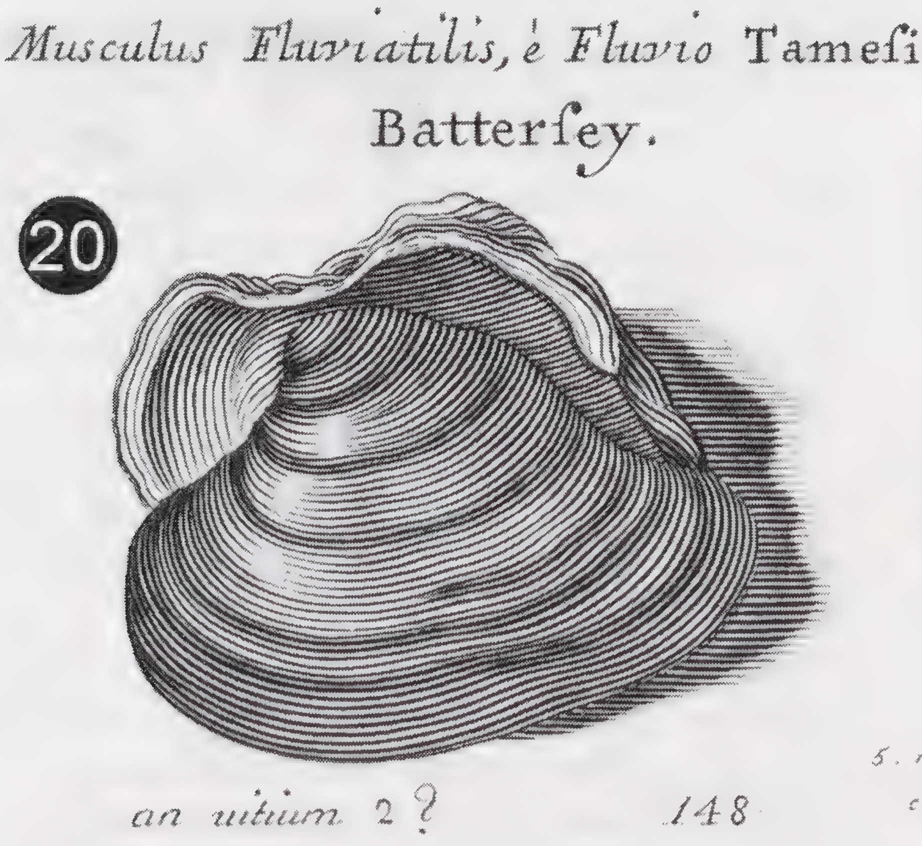

A
2
1. musculus angustior, ex flavo viridescens, medio dorso leviter radiatus, cardinis pinna sive denticulo Birido.

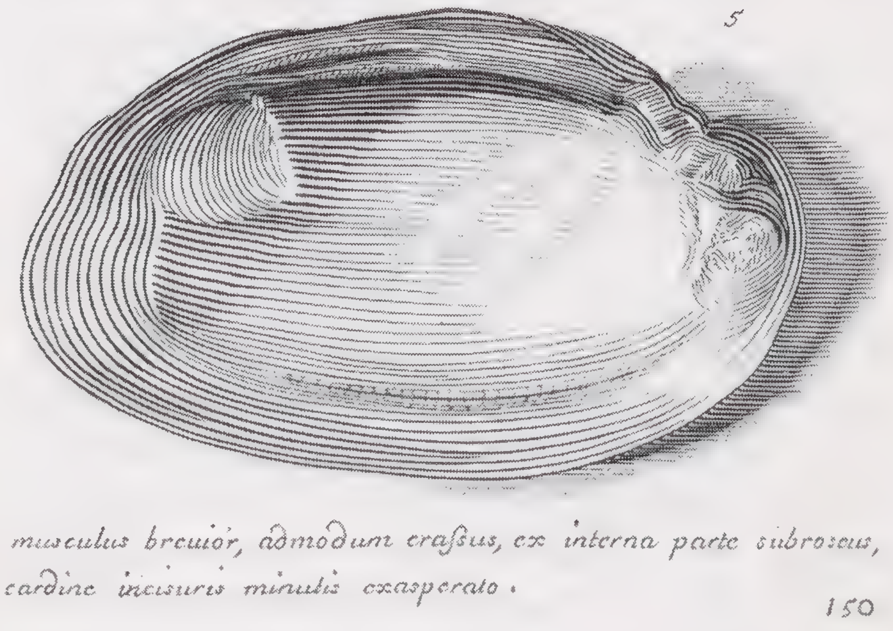

17
A
3
147
3. musculus angustus, subflavus, sive Cirrinus.


Sectio . 2 .
de musculis, cardine Lævi .
A
8
8. musculus tenuis, minor, Subruscus, latiusculus.
19


18
11
A
11 musculus latus, maximus et tenuiſsimus, e coeruleo viridescens fere, palustris.
156




Musculus Fluviatilis, è Fluvio Tameſi Batterſey.
20
an vitium 2?
148


5
5. musculus brevior, admodum craſſus, ex interna parte subroseus, cardine incisuris minutis exasperato.
150

FIGS. 17–21. FIG. 17: Figures of *Unio pictorum* from Lister (1685–1692); FIG. 18: Figure of *Anodonta sp.* from Lister (1685–1692); FIG. 19: Figure of *Anodonta anatina* from Lister (1685–1692); FIG. 20: Figure of an unidentified freshwater mussel, probably a deformed specimen, from Lister (1685–1692); FIG. 21: Figure of an unidentified freshwater mussel from Lister (1685–1692). FIGS. 17–21: By permission of Museo Nacional de Ciencias Naturales, Madrid, Spain.

Duchess of Portland, who collected shells, and was edited by William Huddesford, the curator at the Ashmolean Museum, who saved from destruction the head and one leg of the last stuffed dodo in existence. Lister bestowed on the Ashmolean his collection of British shells, naiads included, as well as the copper plates and the original drawings of *Historia conchyliorum*. In this outstanding work, he included the same figures of naiads before used (Lister, 1685) (Figs. 16–19) and added several new ones (Figs. 20–28), most species from outside England and even Europe, such as the labelled *Pectunculus subviridis, triquetrus* [little greenish, triangular shaped scallop] (Fig. 27), from the *Musaeo Oxoniensis* [Ashmolean Museum], which might be *Cristaria plicata* (Leach) from China or *Potamilus alatus* (Say, 1817) from North America. It is of interest that close to one of these figures, probably representing *Unio tumidus* Philipsson, 1788, and according to its caption *Musculus a Danubio* [mussel from the Danube River] (Fig. 28), Lister also figured what we interpret as a cord of glochidia or freshwater mussel larvae.

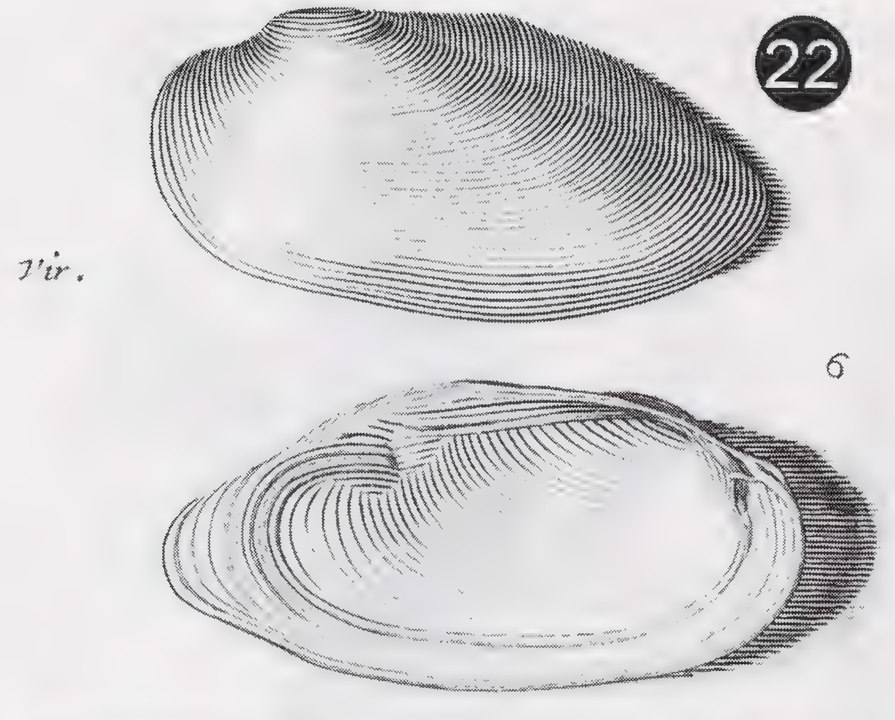
Lister (1696) was also the author of an anatomical picture of a naiad (Fig. 29). The same plate contains images of the glochidia, the ligament, and the aragonite crystals of the inner side of the shell. Nevertheless, the first author who showed the anatomy of a naiad was not Lister but Antonius de Heide (1683). This Dutch medical depicted several isolated parts of a specimen of *Anodonta* in a book that also offered the first description of the cilia motion at the gills and at the cirri around the mussel's mouth (Heard, 1998).

The Dutch Antoni van Leeuwenhoek (1697), who with Heide and Buonanni was an early microscopist, illustrated several naiads (Fig. 30). This work was a sequel to Leeuwenhoek (1695), a collection of studies on microscopy observations written as illustrated letters, most of them dedicated to the Royal Society. The represented species is *Anodonta cygnea* showing its soft parts, eggs and glochidia, which Leeuwenhoek called *Pisciculus testaceus* [small clams]. This author was the first to distinguish the sex of freshwater mussels based on observations of eggs and spermatozoids in different specimens. He also observed eggs passing to the gills and even tried to follow the development of larvae when they were removed from the gills, yet these died shortly after their isolation. The metamorphosis of glochidia into juvenile mussels as parasites of fishes was discovered much later by Houghton (1862) and Leydig (1866). Before these authors, Rathke (1797) wrongly concluded that glochidia were animals that parasitize the gills of fishes and assigned them the spurious specific name of *Glochidium parasiticum* (Heard & Dinesen, 1999).

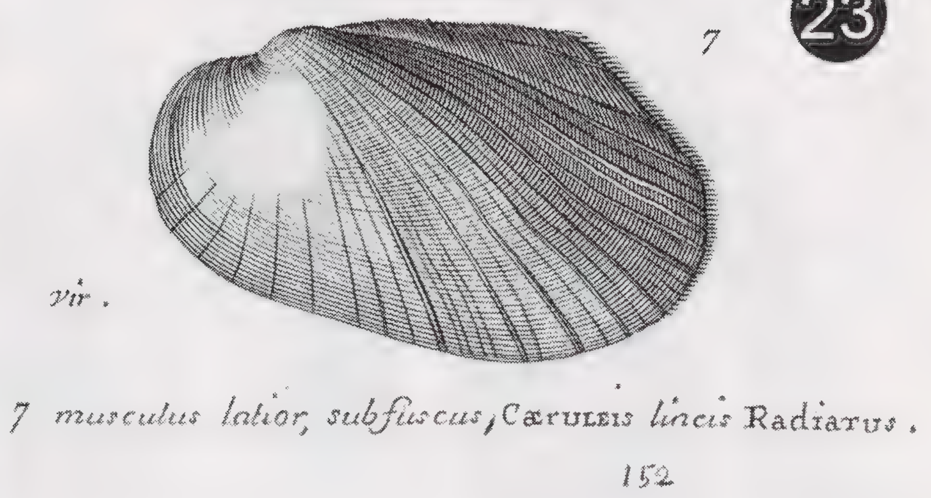
The first living naiad in its own environment was figured by Poupart (1731) (Fig. 31B), who wrote the first natural history of freshwater mussels. This figure was later copied by Scheuchzer (1735). The image shown is one of a semiburied naiad specimen moving forward to create a typical track or furrow in the sediment. Poupart (1731) also depicted two valves of *Anodonta anatina*, a dorsal view of the shell and a detail of its ligament (Fig. 31A).

The next chronological illustration is a curious and anonymous poster kept at the cloister of Ebstorf, Germany (Fig. 32). The poster is dated 1736 and was created for standing at the banks of the Schwienau River in High Saxony. The warning of the more than unpleasant results of violating the prohibition of fishing for freshwater mussels is clearly expressed by an axe, a sectioned left hand and a specimen of *M. margaritifera* with its valves open showing three pearls inside. The legend says *Hüte Dich fur Schaden* [preserve your hands]. Another anonymous illustration related to pearl fishing in High Saxony is a drawing dated *circa* 1760 and entitled *Perlen-Sucher in seinem Wasser-Habit* [pearl searcher in his water outfit] (Fig. 33). The subject, who is accompanied by a poodle or water dog, has a pearl mussel in his left hand while in the right carries a large wooden forceps to collect submerged naiads. He also carries a musket on his back for hunting and protection from bears, which were then more abundant than now along the Paleartic waterways inhabited by *M. margaritifera.* At this point, mention should be made of a pencil sketch by Linnaeus. The drawing (Fig. 34) appeared in *Iter Lapponicum* or *Journey to Lapland*, a hand-written account of his trip to Lapland in the summer of 1732. The journal was found in 1953 during the repair of the building at the botanical gardens of the University of Uppsala, where Linnaeus lived for over 30 years. The sketch of a pearl fishery at a place called Purkijaur depicts a man on a simple raft anchored to the bottom fishing for freshwater mussels using a large forceps. Close to him is outlined a specimen of *M. margaritifera*. In the related text, Linnaeus reflects on the idea of inventing a method to induce the formation of pearls in freshwater

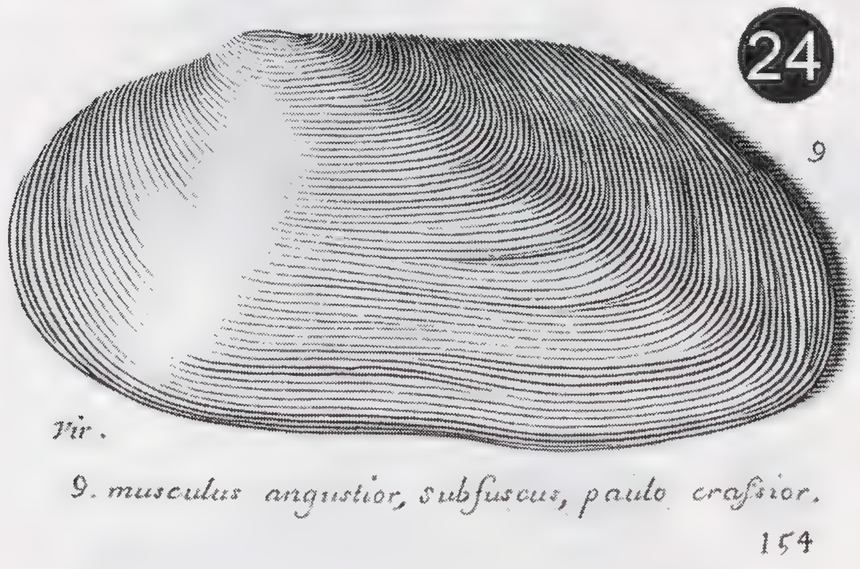
22


Vir.
6
6. musculus fuscus, angustior, ex altera parte Cuneatim protensus.

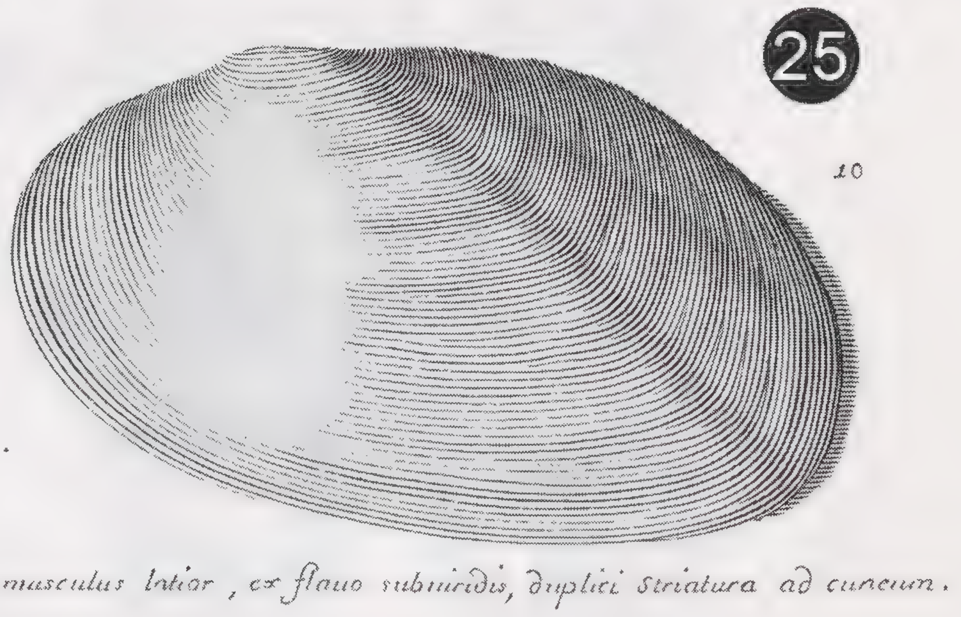
23


7
vir.
7 musculus latior, subfuscus, Cæruleis lineis Radiatus.
152

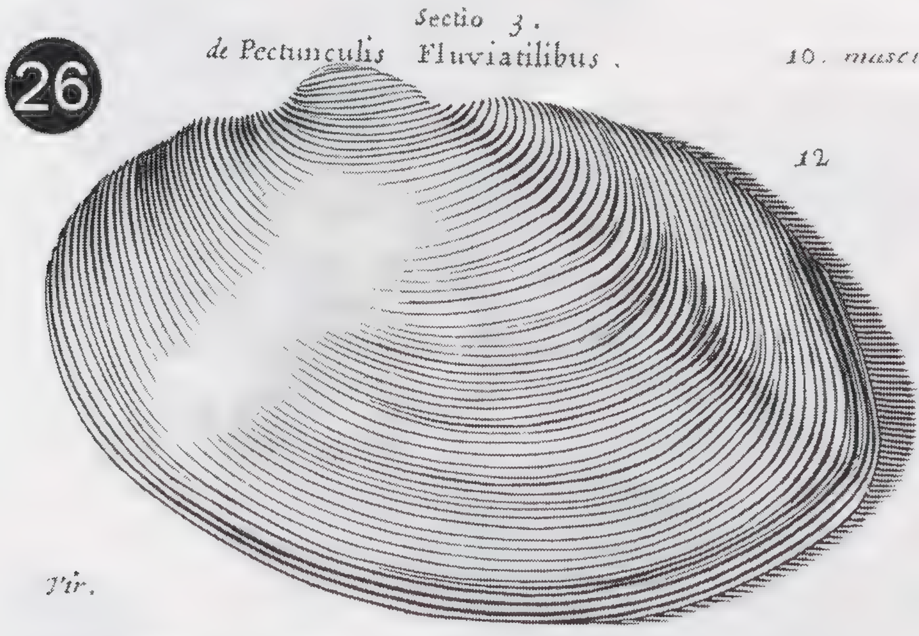
24


9
Vir.
9. musculus angustior, subfuscus, paulo crassior.
154

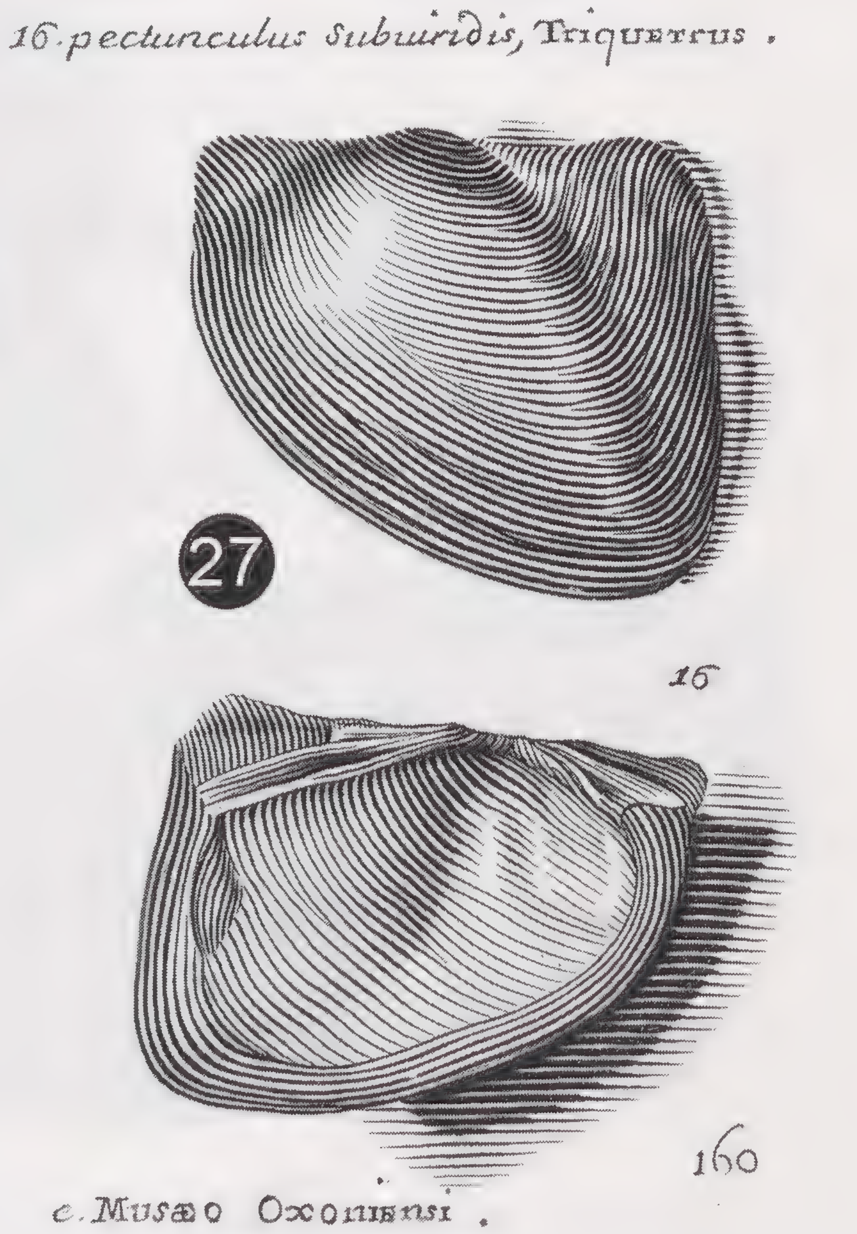
25


10
r.
10. musculus latior, ex flauo subuiridis, duplici striatura ad cuneum.

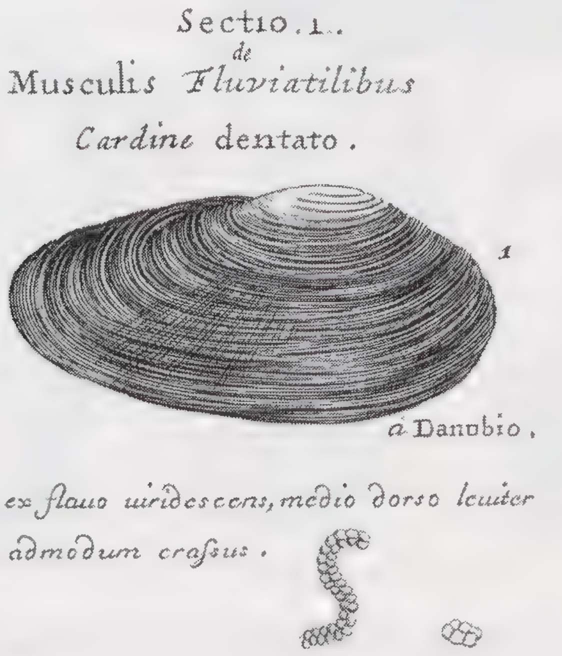
26


Sectio 3.
de Pectunculis Fluviatilibus.
12
Vir.
12. pectunculus tenuis, subruber ex internâ parte, rostro recuruo.
157

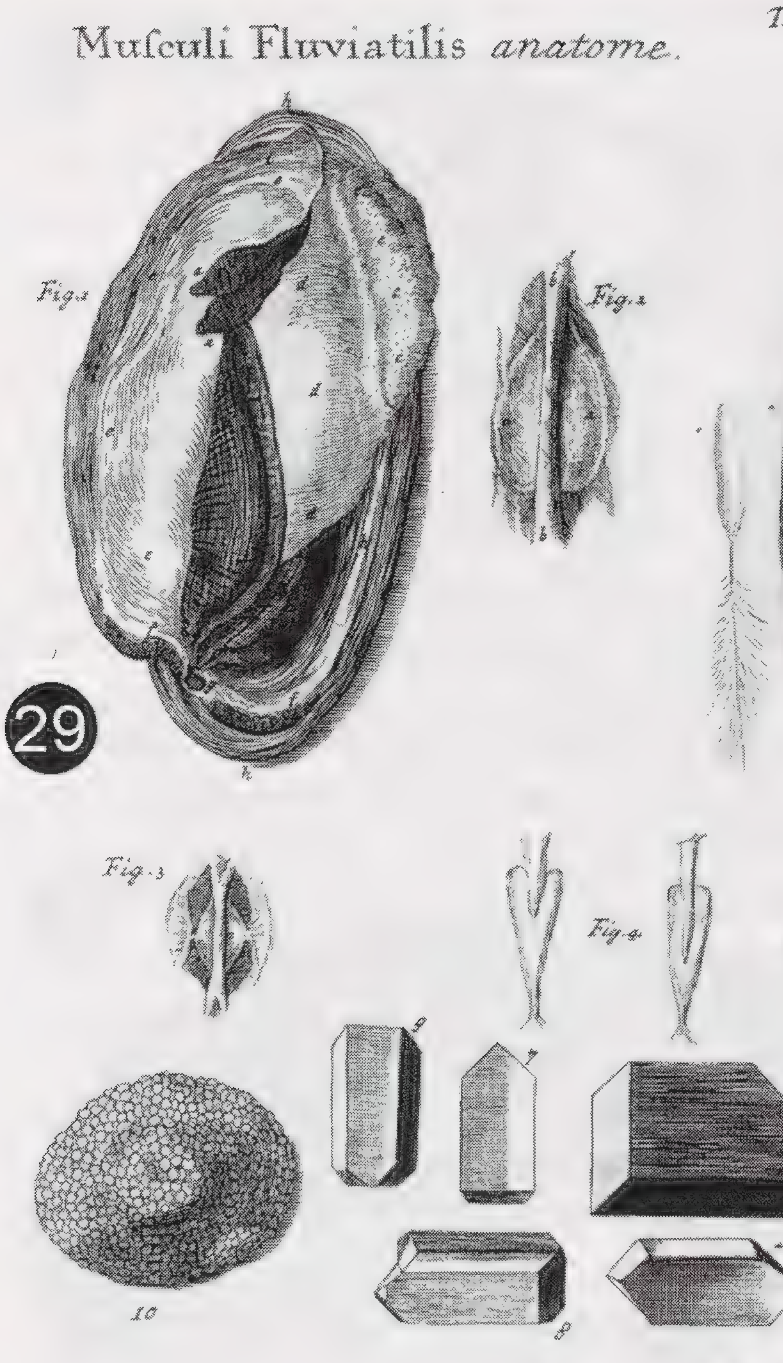
27


16. pectunculus subuiridis, Triquetrus.
16
160
e. Musæo Oxoniensi.

28

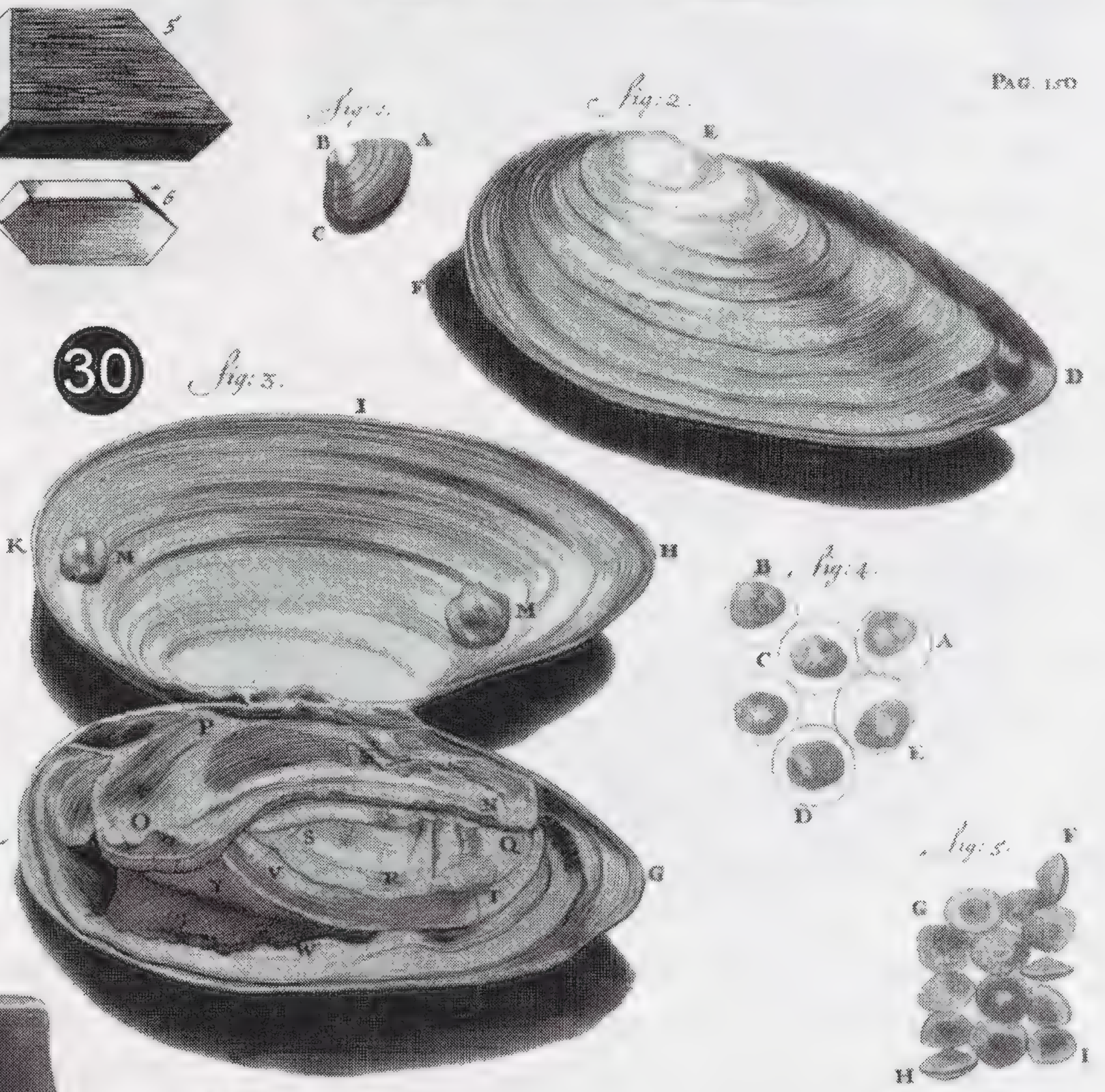

Sectio. 1.
de
Musculis Fluviatilibus
Cardine dentato.
1
a Danubio.
1. musculus ex flauo uiridescens, medio dorso leuiter Radiatus, admodum crassus.

FIGS. 22–28. FIGS. 22–26: Figures of several unidentified freshwater mussels from Lister (1685–1692); FIG. 27: Figure of an exotic freshwater mussel from Lister (1685–1692); FIG. 28: Figure of *Unio tumidus* and glochidia from Lister (1685–1692). FIGS. 22–28: By permission of Museo Nacional de Ciencias Naturales, Madrid, Spain.


29

31a

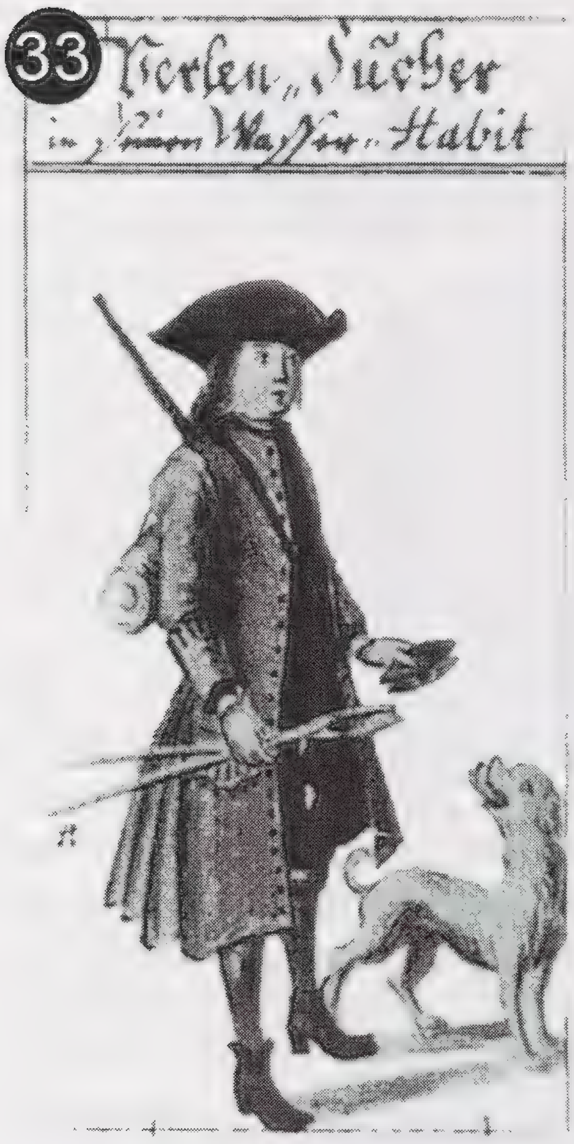
31b


30

32

FIGS. 29–32. FIG. 29: External anatomy of a freshwater mussel and images of its glochidia, ligament and aragonite crystals of the shell from Lister (1696); FIG. 30: Images of a freshwater mussel, its soft parts, eggs and glochidia from Leeuwenhoek (1697); FIG. 31 A: *Moule* from Poupart (1731); B: Freshwater mussel showing its track in the sediment from Poupart (1731); FIG. 32: German anoymous poster (1736). Original at Kloster Ebstorf (Germany). FIGS. 29, 30: By permission of Biblioteca Nacional, Madrid, Spain; FIG. 31: By permission of Museo Nacional de Ciencias Naturales, Madrid, Spain.

33



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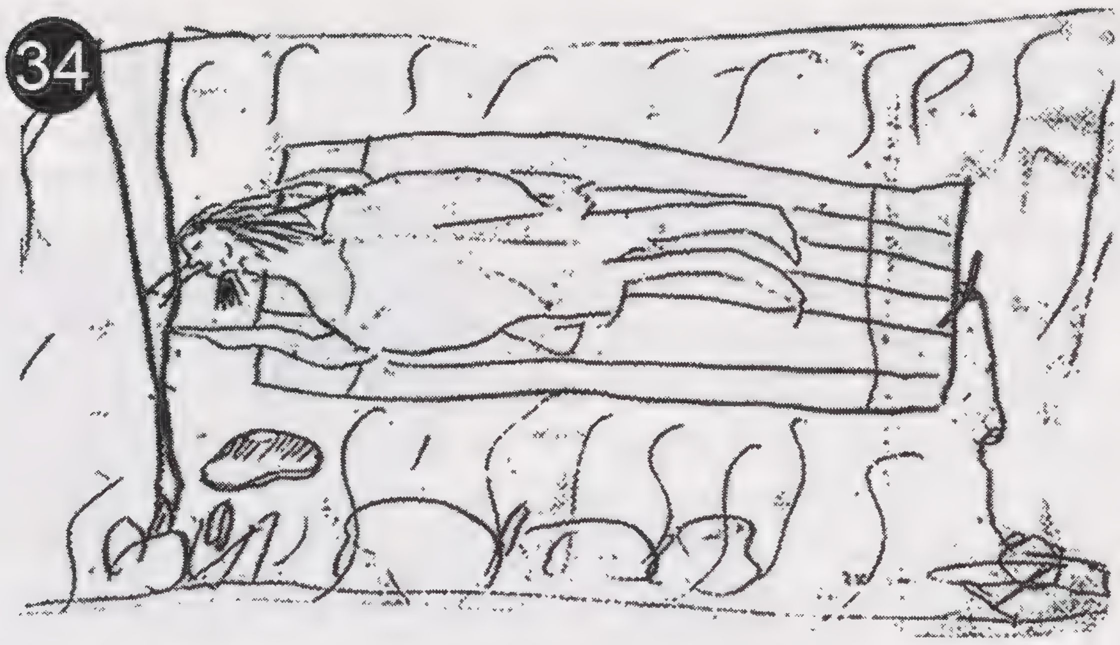
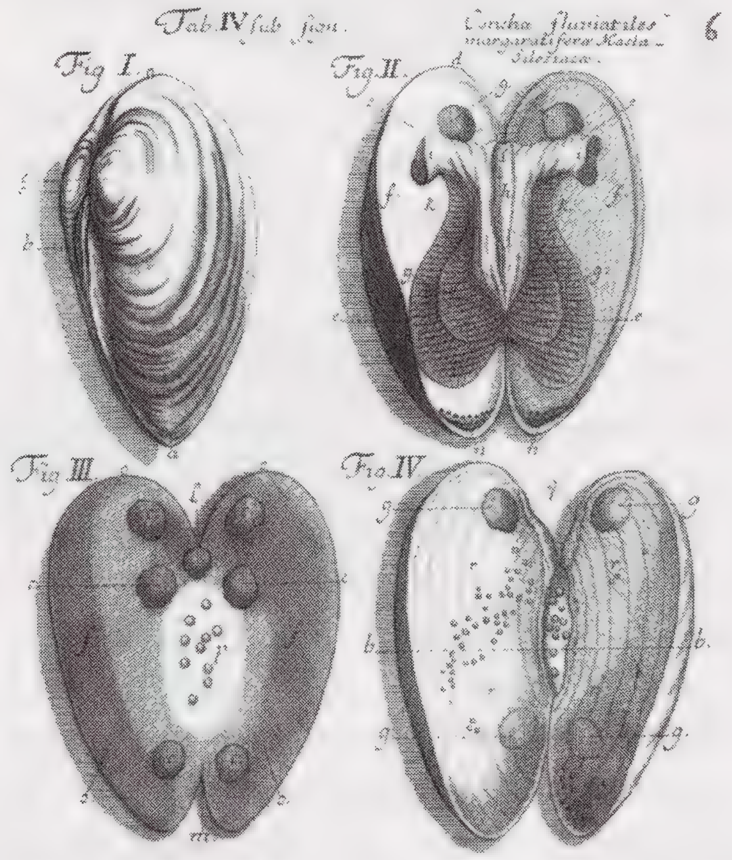
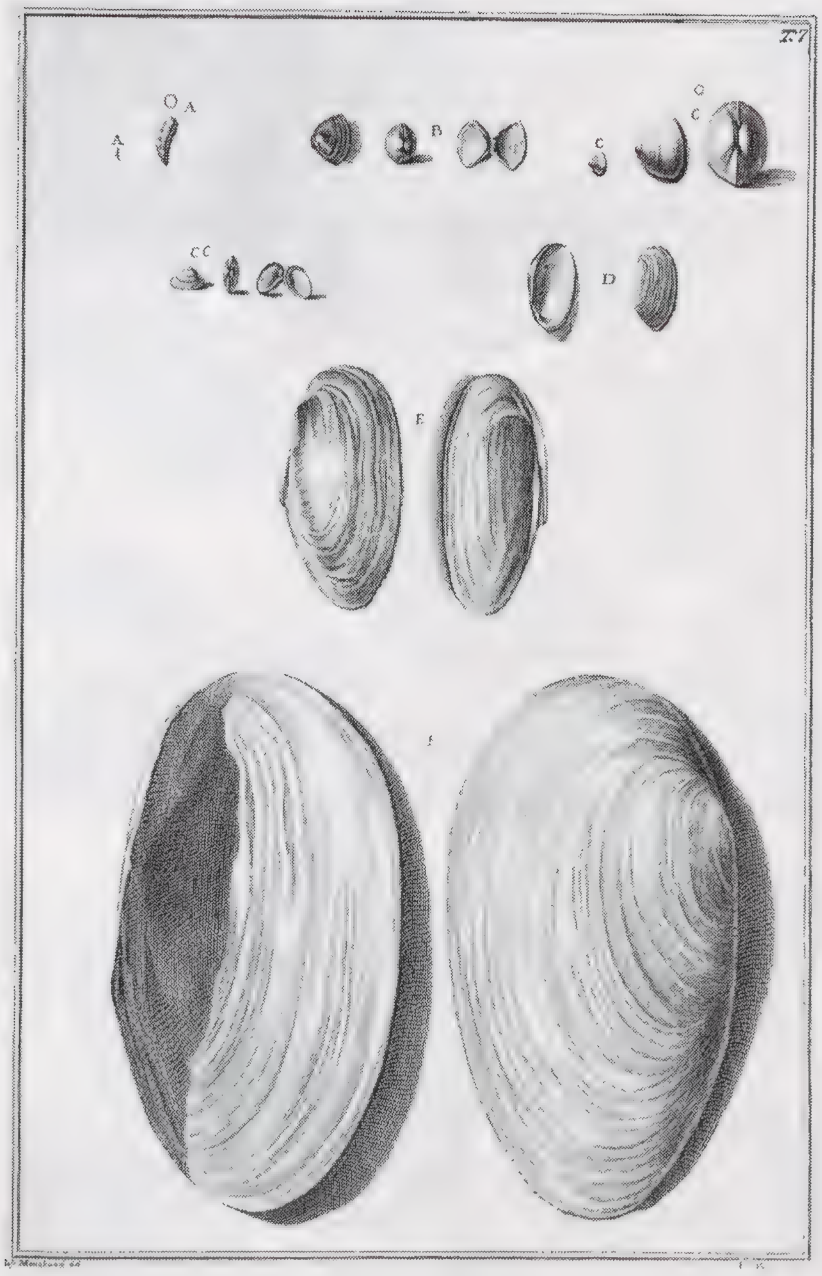


35


Tab. IV sub fin.
6
Fig. I.
Fig. II.
Fig. III.
Fig. IV.

36



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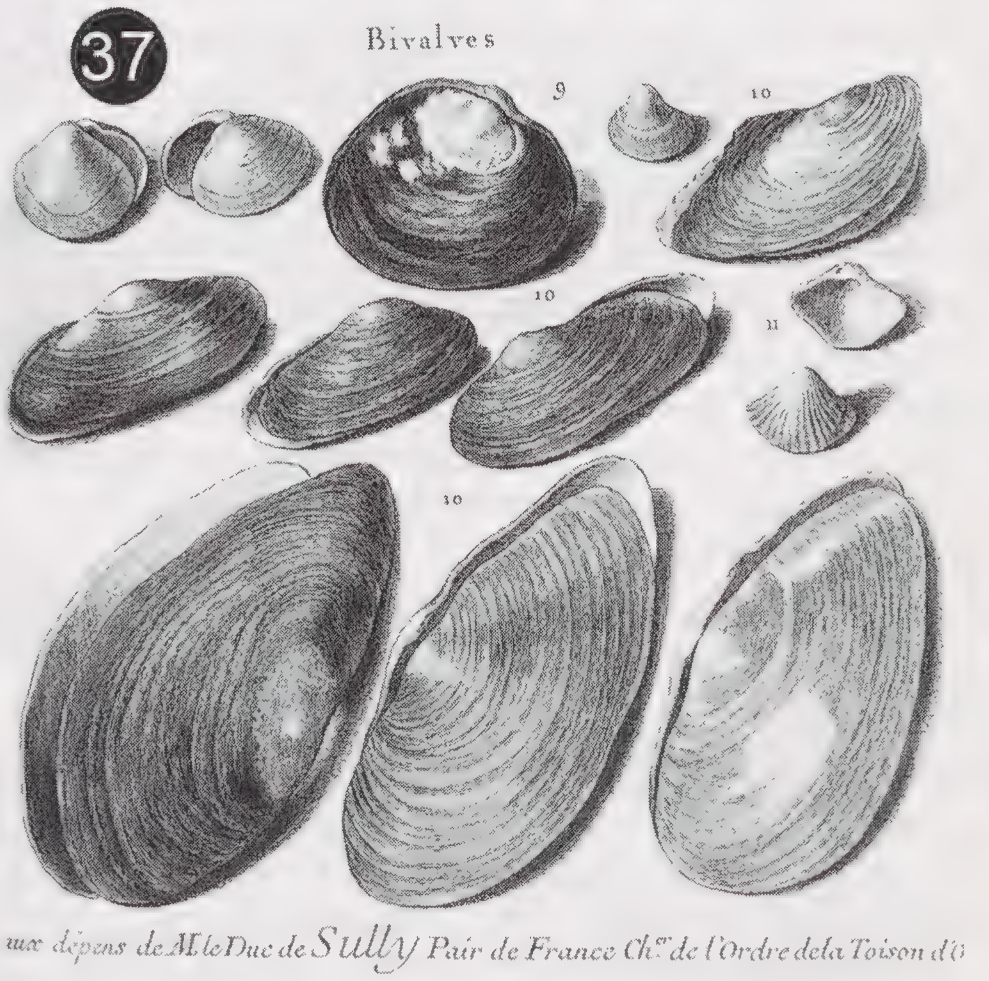

Bivalves
9
10
11
aux dépens de M. le Duc de Sully Pair de France Ch.er de l'Ordre dela Toison d'O

FIGS. 33–37. FIG. 33: German anonymous drawing (*circa* 1760). Original at K. H. Reger collection (Germany); FIG. 34: Pencil sketch by Linnaeus (1732). Original at University of Uppsala (Sweden); FIG. 35: *Concha fluviatiles margaritifera* from Hermann (1737); FIG. 36: *Musculis fluviatilis* from Gualtieri (1742); FIG. 37: *Moules* from D'Argenville (1742). FIGS. 35–37: By permission of Museo Nacional de Ciencias Naturales, Madrid, Spain.

mussels after a comment that the fishery at Purkijaur had been practically depleted, with thousands of mussels unnecessarily killed because there was no way of knowing if they contained pearls or not.

In the 18th century, a number of opuscules and disquisitions speculating on the origin of pearls and their nature were published. Most of these lacked any drawings of naiads or any illustrations. An exception is one by a Leonhard David Hermann (1737) on the freshwater pearl shells of Silesia (Fig. 35). Four different images appear representing the inner and outer sides, the soft parts and the pearls of *M. margaritifera*.

The Florentine physician and naturalist Nicoló Gualtieri (1742), physician to Duke Cosimo III of Medici and a shell collector, figured several specimens of *Anodonta* and *Unio* (Fig. 36). That same year saw the publication of the first edition of *La conchyliologie* by Antoine Joseph Dezallier D'Argenville (1742), a councilman of King Louis XV of France who also collected shells. Several figures of naiads are there included (Fig. 37). According to the text, most of them were from the French rivers Gobelins, Loire, Marne, and Seine, but others seemed to be from North America. The second and third editions of this book, published in 1757 and 1780, were different. They added an anatomy section in which three specimens of *Unio* and *Anodonta* showing their feet were figured (Fig. 38). The third edition, post-Linnean in age, was prepared by the father and son editors Favanne de Montçervelle and included a beautiful plate with 30 figures of naiads symmetrically positioned in Rococo style (Fig. 39).

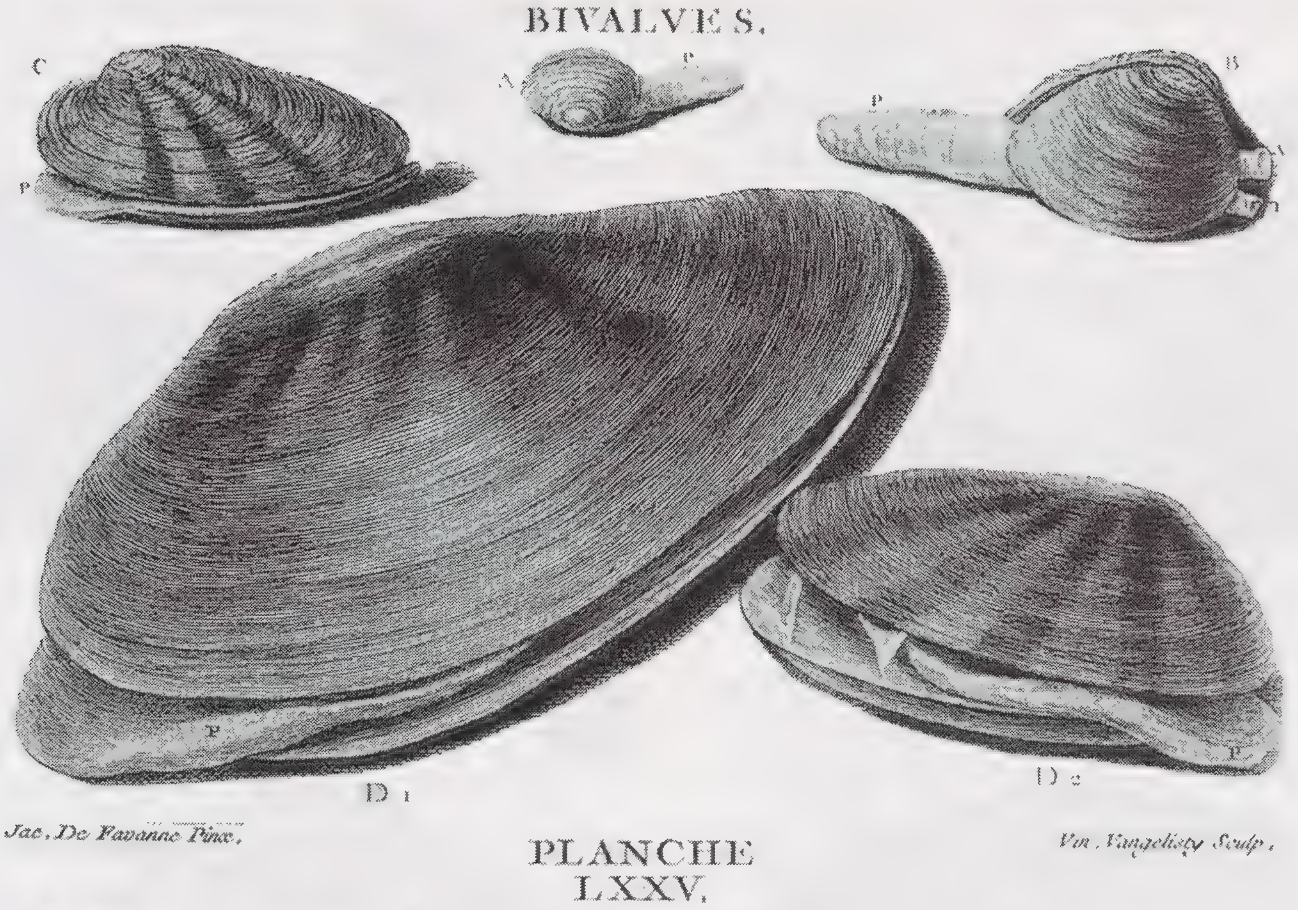
Images of naiads abide in publications of the second half of the 18th century. An illustration of *Unio* by the Dutch physician and entomologist Jan Swammerdam (1737) appeared in *Bybel der Natuure* (Fig. 40). This illustration only showed the anatomy of the species, as expressed by its caption, which says *Mytuli concha, interna representata* [shell of mussel internally depicted]. Another *Unio* was figured by the Earl Luigi Ferdinando Marsigli (1744) in the second volume of his *Description du Danube* (Fig. 41), a luxury encyclopaedia on the Donau River. Identical to the pictures of *Margaritifera* and *Anodonta* by Lister (1685, 1685–1692) were those figured by Jakob Theodor Klein (1753). This author, secretary of the Senate of Danzig, Germany, respectively named them *Diconcha sulcata* (Fig. 42) and *Musculus latus* (Fig. 43). Another *Unio* (Fig. 44) was figured among several marine bivalves by Frans Valentijn (1754), who was a priest at the Dutch colony in Ambon, Moluccas, and wrote a supplement to *D'Amboinsche Rariteitkamer* by Rumpf (1705). Erik Ludwigsen Pontoppidan (1755), bishop of Bergen, Norway, depicted *M. margaritifera* with two pearls (Fig. 45). Several naiads of the genera *Anodonta* and *Unio*, designated *Conca de Pittori* (Figs. 46, 47), were depicted by the Earl Giuseppe Ginanni (1757), also including a representation of glochidia. Finally, an image of an African freshwater mussel belonging to the genus *Mutela* (Fig. 48) was figured by Michael Adanson (1757). This author refers to the drawing as *Le mutel* and mentions it was fished in the lakes of Senegal.

The last illustration of a naiad we considered is also the first coloured one (Fig. 49). It appears in Georg Wolfgang Knorr's *Vergnügen der Augen und des Gemüths*, a book printed in 1757–1773, its French version edited in 1760–1773 as *Les délices des yeux et de l´esprit*, paraphrasing Buonanni (1681). Knorr worked as an engraver in Nuremberg, Germany. From a purist perspective, we must say this nice drawing of a naiad, water-coloured by hand and clearly inspired by the pictures by Gessner (1558) and Lister (1685, 1685–1692), is ten years post-Linnean because the fourth part of the book by Knorr, where it is, was not printed till 1769. The figure depicted is the inner side of a left valve of *M. margaritifera* showing the hinge, the pallial line, the two adductor muscle scars and the reflections from the nacre. Its caption says *La moule a perles de l'Elster* [the pearl mussel from the Elster River] and it adds *Ex Museo Mülleriano* [from Müller's collection].

ILLUSTRATION OF LIVING FRESHWATER MUSSELS, THEIR SOFT PARTS, EGGS AND GLOCHIDIA

As we have seen, living naiads or details of their anatomy were scarcely depicted in pre-Linnean times (Table 1). Adanson (1757) criticized shell collectors for their lack of scientific interest in the study of molluscs, which he pointed out to be humble animals in their external aspect but able to construct such beautiful shells, noting that conchology can be only viewed as one aspect of malacology: "The same beauty of shells that induced the interest for them has become a serious obstacle for the progress of natural history".

38



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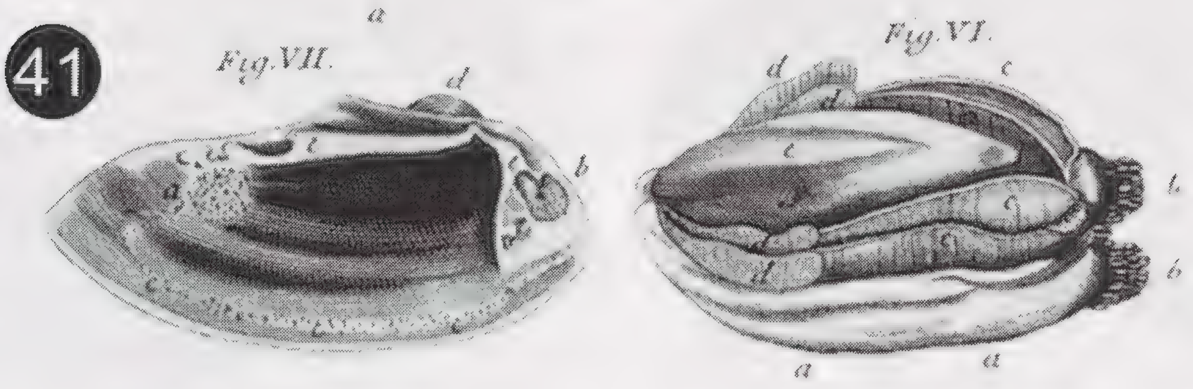

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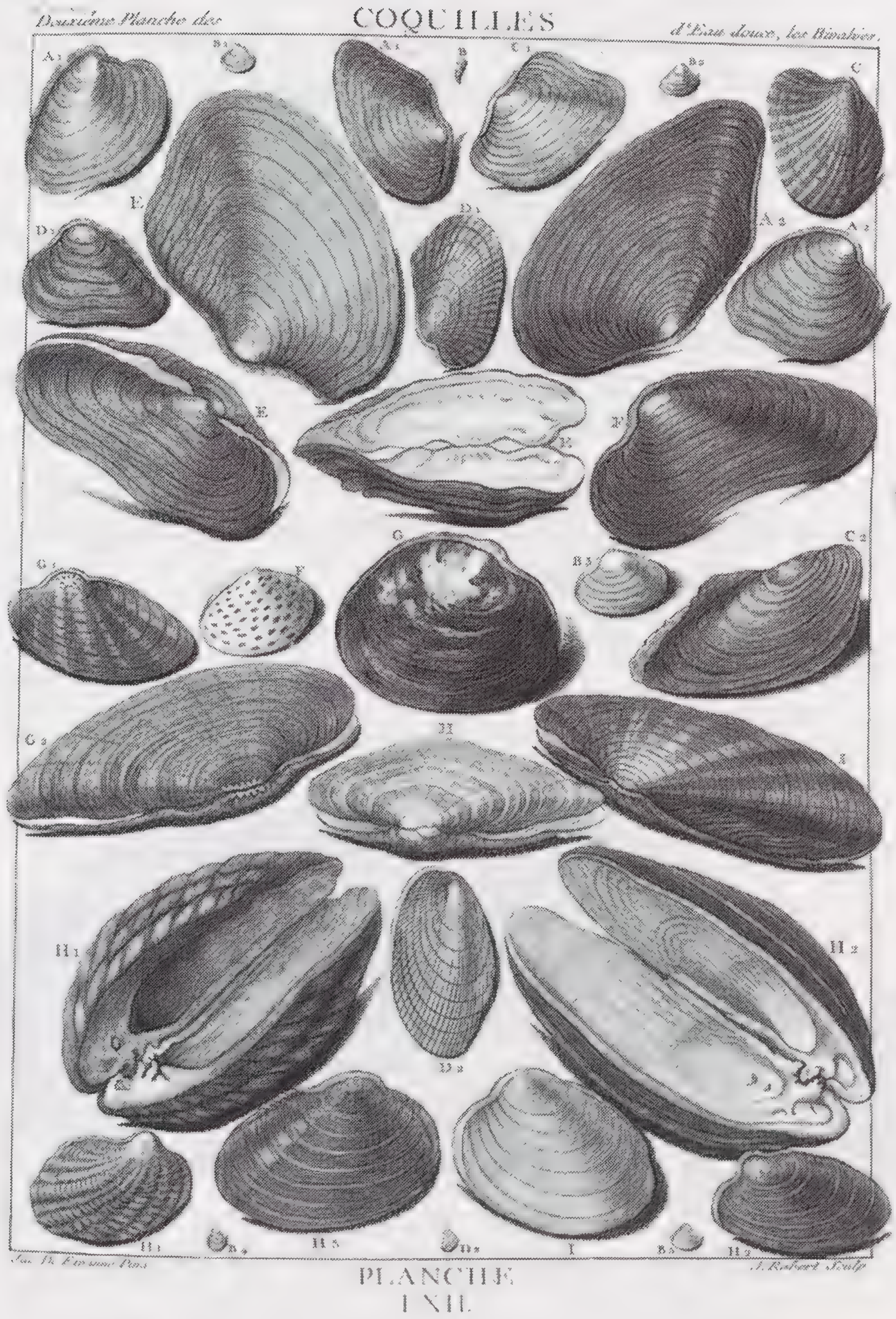

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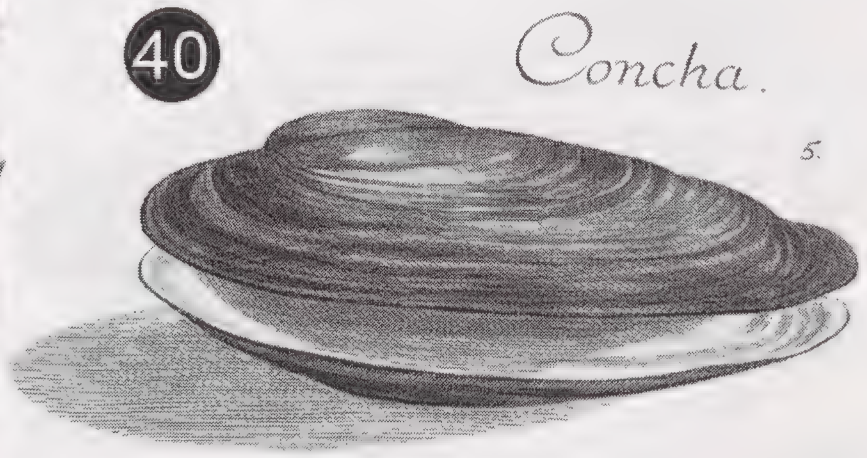

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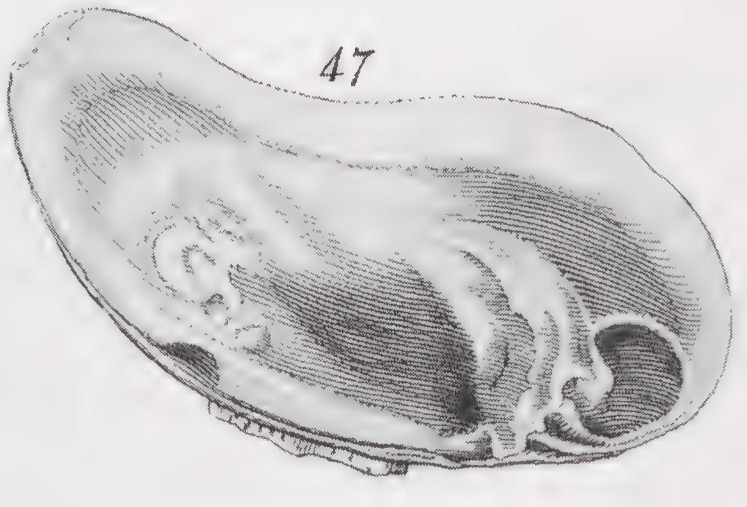
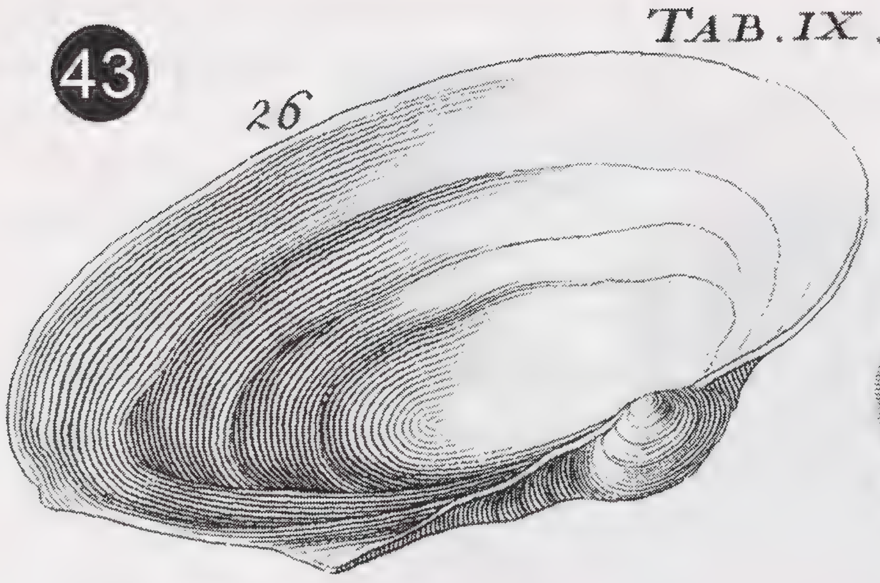


FIGS. 38–42. FIG. 38: *Moules* from D'Argenville (1757); FIG. 39: *Moules* from D'Argenville (1780); FIG. 40: *Moule* from Marsigli (1744); FIG. 41: External anatomy of a freshwater mussel from Swammerdam (1737); FIG. 42: *Diconcha sulcata* from Klein (1753). FIGS. 38, 39, 40, 42: By permission of Museo Nacional de Ciencias Naturales, Madrid, Spain; FIG. 41: By permision of Biblioteca Nacional, Madrid, Spain.

43



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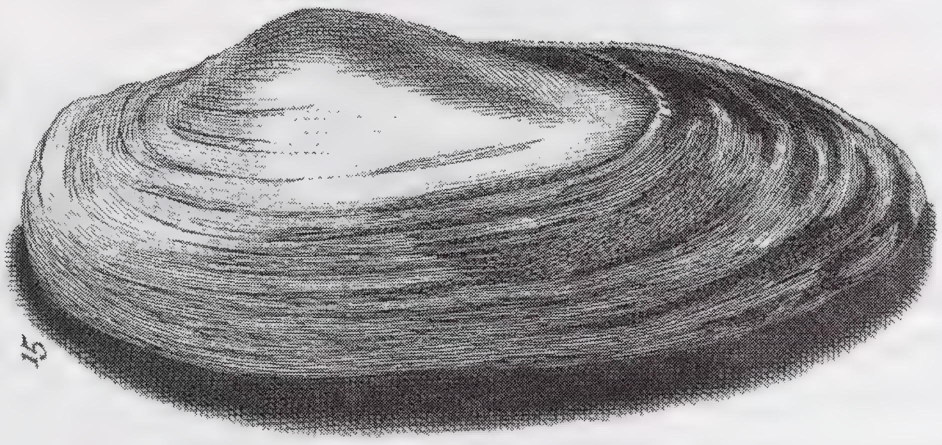

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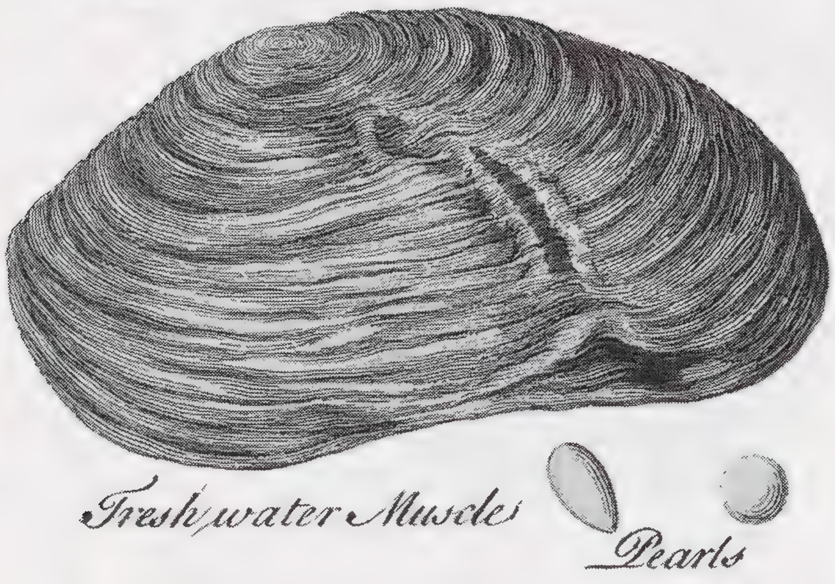

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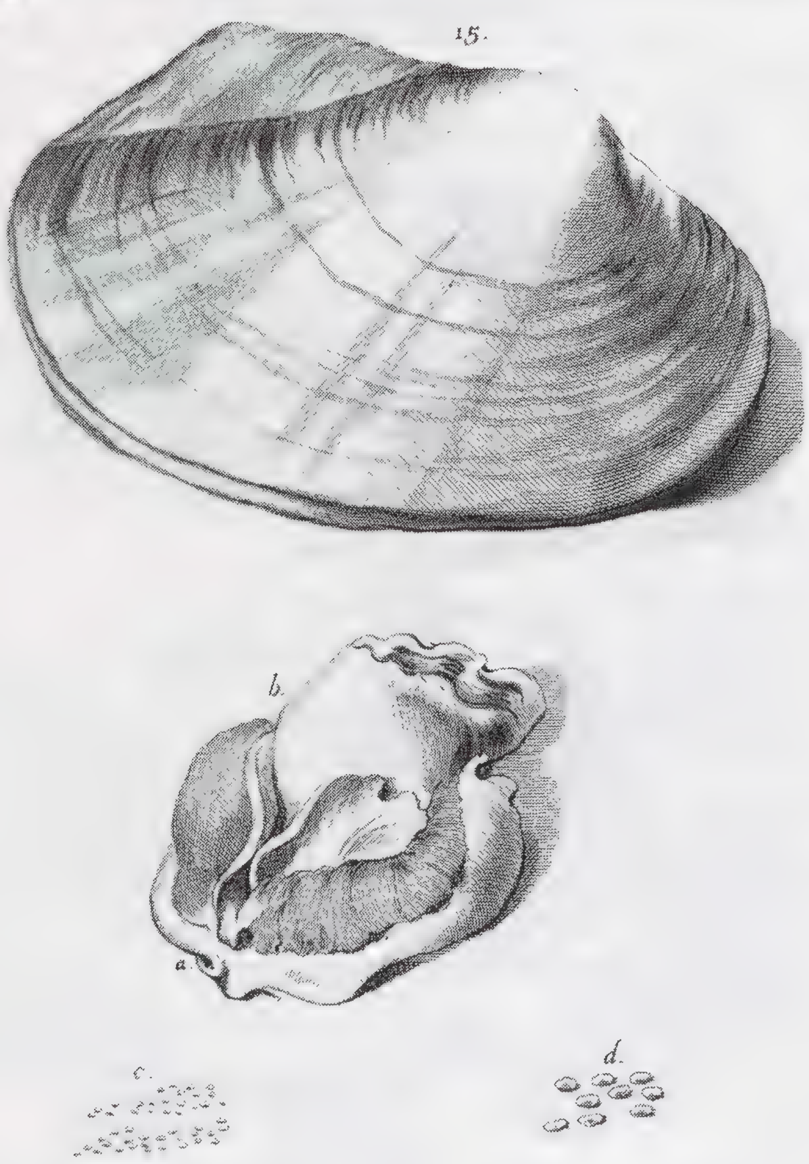

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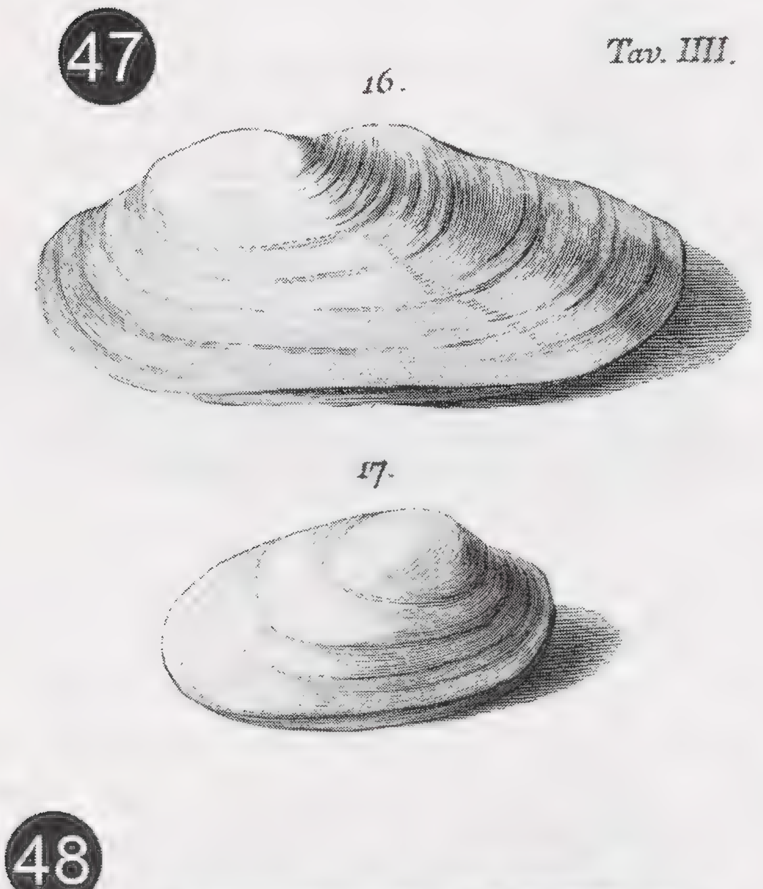
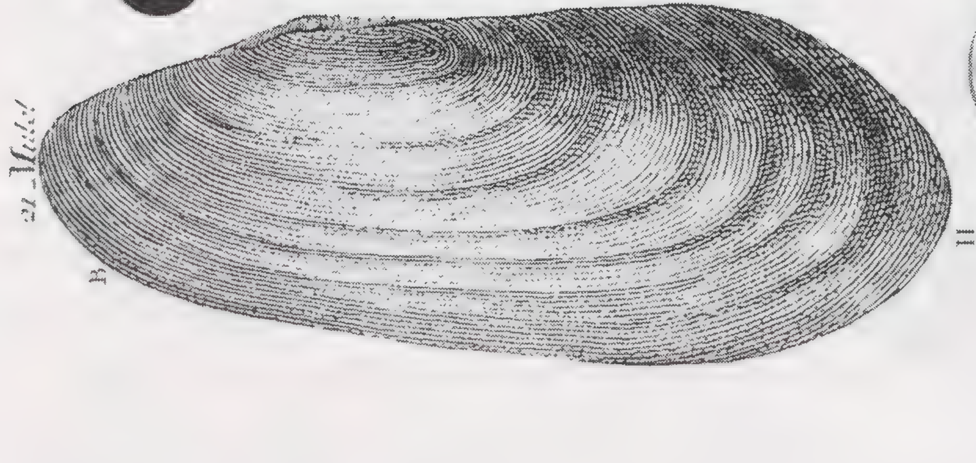
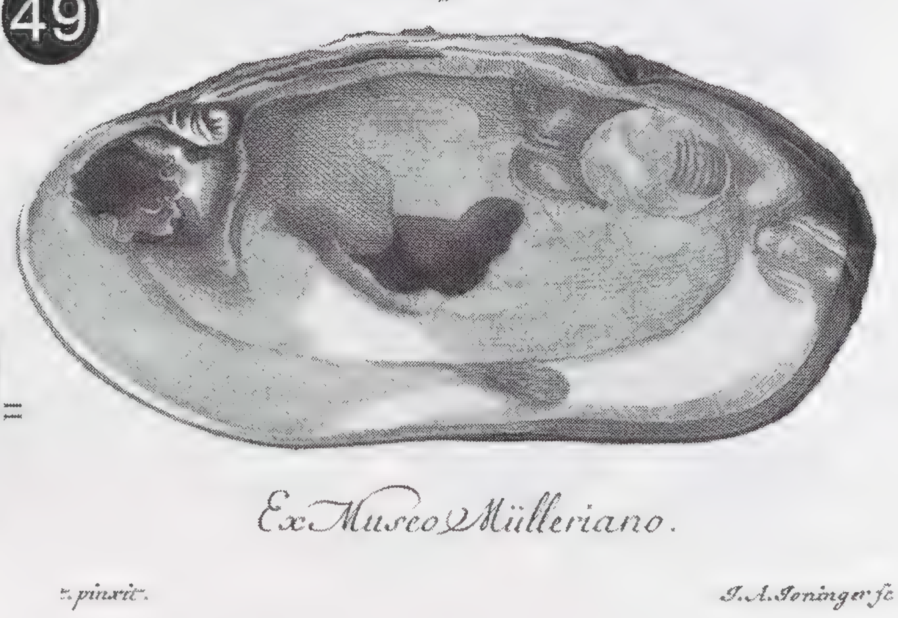


48



49


2
Ex Museo Mülleriano.
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J.A.Joninger fc.

FIGS. 43–49. FIG. 43: *Musculus latus* from Klein (1753); FIG. 44: Unnamed figure from Valentijn (1754); FIG. 45: *Freshwater muscle* and two pearls from Pontoppidan (1755); FIG. 46: *Conca de Pittori* from Ginanni (1757); FIG. 47: *Conca de Pittori* from Ginanni (1757); FIG. 48: *Le mutel* from Adanson (1757); FIG. 49: *La moule a perles de l'Elster* from Knorr (1768). FIGS. 43–49: By permission of Museo Nacional de Ciencias Naturales, Madrid, Spain.

A similar argument in favour of anatomical studies on molluscs was also put forward by D'Argenville (1757), who also implored naturalists to take more interest in living molluscs in admiration for the creations of God.

Heide (1683) presented the first known illustrations of the anatomy of naiads (Heard, 1998). Later ones were provided by Lister (1695), Leeuwenhoek (1697), Hermann (1737), Swammerdam (1737), D'Argenville (1742), and Ginanni (1757). Some of these authors also illustrated the eggs, glochidia and the microscopical architecture of the shells. The only pre-Linnean picture of a living naiad was the drawing by Poupart (1731) discussed above, which was copied by Scheuchzer (1735).

Giuseppe Saverio Poli was the first author who figured the gonad, siphons, gill structure, eggs, and glochidia of naiads in a modern way. The elaborate and lavish plates in the three volumes of his *Testacea utriusque Siciliae*, printed in 1791–1827, are among the most beautiful illustrations of the external appearance and anatomy of freshwater mussels. They are not considered here because that book is clearly post-Linnean. The same occurs with the illustrations by both Etienne Louis Geoffroy (1767) and Johann Samuel Schröter (1779). Schröter published *Die Geschichte der Flussconchylien*, the first book entirely devoted to freshwater molluscs. Its first five plates, hand-coloured in some copies, illustrated practically all the European species of naiads as well as other bivalve species of the families Sphaeriidae and Corbiculidae. Missing was *Margaritifera auricularia* (Spengler, 1793), which despite its discovery and naming by the Danish malacologist Lorentz Spengler, continued to be confused with the pearl-producing, much more depicted *M. margaritifera* (Valledor & Araujo, 2006).

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